JOURNAL OF AVIAN BIOLOGY 36: 501–509, 2005

Colony specific variation in the use of a moulting site in the migratory little tern *Sterna albifrons*

Giacomo Tavecchia, Nicola Baccetti and Lorenzo Serra

Tavecchia, G., Baccetti, N. and Serra, L. 2005. Colony specific variation in the use of a moulting site in the migratory little tern *Sterna albifrons*. – J. Avian Biol. 36: 501–509.

Individual-based data on little terns *Sterna albifrons* at a post-breeding moulting area were used to investigate the spatial extent at which this site attract birds. Combining information collected on young terns, ringed at the natal colonies, with that on birds captured a few months later at the moulting site, we estimated a survival/movement parameter for each age-by-colony combination. This parameter is the product between the survival probability and the probability to visit the moulting site. The distance between the natal colony and the moulting site negatively influenced the probability of reaching the site in yearlings. Having corrected for the distance from the moulting area, colony characteristics explained only about 10% of the spatial variation in the survival/movement parameter of juveniles. In older birds that had visited the site at least once in their life, neither the colony nor the distance affected the survival/movement parameter significantly. The average annual adult survival/movement probability was 0.90. Juvenile survival between June and September was 0.60. Overall results suggest that the moulting area could act as a 'population funnel' within a system of moult migration that involves birds breeding up to 500 km away. However, other unknown moulting site must exist within this area that could be important for the conservation of the species.

G. Tavecchia (correspondence), Institut Mediterranei D'Estudis Avançats – CSIC/UIB, c. M. Marques 21, 07190, Esporles, Spain. E-mail: g.tavecchia@uib.es. N. Baccetti and L. Serra, Istituto Nazionale per la Fauna Selvatica, Via Ca' Fornacetta 9, 40064 Ozzano dell'Emilia, Bologna, Italy.

Much information on avian migratory strategies is collected at particular sites where individuals converge to refuel during migration, i.e. stopover sites (Frederiksen et al. 2001, Gauthier et al. 2001, Schaub and Jenni 2001, Schaub et al. 2001), or to complete feather replacement, i.e. moulting sites (Hötker and Frederiksen 2001). These sites act as 'population funnels', attracting individuals from very large areas. They give a unique opportunity to obtain a snapshot of populations otherwise dispersed over vast areas (Boere 1976, Jehl 1988). A peculiarity of moulting sites is that they may represent the goal of separate movements, differently oriented from true migration routes. The so-called moult migrations are usually directed to sites with low predation pressure and abundant food resources (Salomonsen 1968, Jehl 1990), to deal with the high energy demands of feather replacement, increased flying costs and greater vulnerability (Jehl 1990, Murphy 1996, Swaddle et al. 1996, Swaddle and Witter 1997, Hedenström and Sunada 1999). The location of the moulting areas and the extent to which these sites attract individuals from different breeding areas are often unknown. Yet, this has very important consequences for population dynamics and conservation strategies. For waterbirds in particular, the need of preserving the main stopover sites along each flyway has long been recognised (Szijj 1972, des Clers 1976, Smit and Piersma 1989, Evans et al. 1991), and is a high priority in the general strategy of bird conservation. Stopover and moulting sites expose populations to high risks, as shown by species or populations threatened by factors acting at non-breeding sites (Archibald and Landfried 1993, Madsen 1996).

A large post-breeding roost of little terns *Sterna albifrons* discovered in the Lagoon of Venice, Italy, was the goal of a moult migration. Thousands of birds moved in a mainly northern direction from their colony sites before finally departing on a south-west route towards the winter quarters (Cherubini et al. 1996). The little tern is a small, long-distance migratory waterbird that breeds colonially along seashores, on river banks and in lagoons throughout the Mediterranean basin and Northern Europe. Since 1990 the species has declined throughout its European range and it is locally threatened by human pressure along seashores and the largest rivers (Fasola et al. 2002). The European population is thought to spend the winter along the western coasts of Africa (Cramp 1985, Muselet 1985). After breeding, adults undergo a moult process that may simultaneously involve two series of primary feathers. Feather replacement is temporarily suspended to allow a 7,000 km journey (Cherubini et al. 1996). Juveniles follow adults for several weeks after the colonies are vacated and, despite starting moult later, also visit the moulting areas (Serra 1993, Cherubini et al. 1996). Recaptures of ringed birds proved that moulting flocks in the Lagoon of Venice attract adults and juveniles from a basin that encompasses the entire eastern Adriatic coast (Cherubini et al. 1996). A large number of colonies fall within this range, hosting a total of about 6,000 pairs that makes Italy rank first among European countries for this species (Fasola et al. 1989, Muselet 1997). However, recent censuses suggest a decrease of the Italian population due to breeding habitat loss and human disturbance (Cherubini et al. 1996, Fasola et al. 2002). The high concentration of birds at this site, and a high risk of habitat loss due to inappropriate site management and to a direct negative impact from the construction of a tide regulation system protecting Venice city from high waters (Bourdeau et al. 1998, Ravera 2000, Pirazzoli 2002), suggested an opportunity for further analyses of its role and significance at larger scale. In this paper we investigated the extent to which the colony of birth influenced the probability of reaching the moulting site by combining the information collected from multiple breeding colonies with that obtained at the moulting site. Moreover, the capture-recapture data provided an opportunity to estimate little tern post-fledging and annual adult survival probabilities for the first time.

Material and methods

Ringing programme and capture-recapture data

From 1990 to 1997 little terns were individually marked with metal rings supplied by the Italian bird ringing centre. Data were merged from two different sources. The first part of the information came from birds ringed as chicks at the main Adriatic breeding colonies (Fig. 1 and Table 1), where several ringers started independent activities in different years. The second set of data is made up of juveniles and adults captured after the breeding season at a roosting site in the Venice Lagoon (Fig. 1). Birds were caught with mist-nets during the night, two to four months after breeding ended. The majority of these individuals were in active moult and the roosting site was visited from late June to mid September, when the last terns migrated to wintering quarters (Cherubini et al. 1996). For the sake of simplicity we will refer to this site as the ‘moulting site’. Here we captured three categories of individuals: i) juveniles marked as chicks earlier in the season at their natal colony, ii) adults marked in previous years, either as chicks at the natal colony, or as juveniles/adults at the moulting site, and iii) unmarked birds (adults and juveniles).

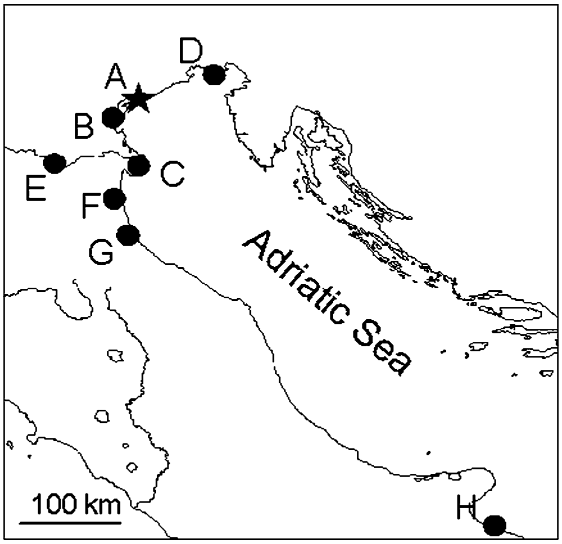

Fig. 1. Individuals were marked as fledglings early in the year at different breeding locations (solid circles, B-H) and at a nocturnal roosting site used during the post-breeding moult (star, A).

Table 1. Ringing totals per area and years of activity. Areas are ordered according to increasing distance from the moulting site (A). For each location, coordinates are from one of the colony only.

	Location	Colony	Coordinates	Distance from A (km)	Ringing period	Ringing totals
A	Lagoon of Venice	Sant'Erasmo	45.27°N, 12.25°E	0.00	90–97	3400
B	Lagoon of Venice	Settemorti, Pellestrina, Fondello, Ca' Roman	45.15°N, 12.13°E	25.0	91–96	352
C	Po delta	Barricata, Barbamarco	44.58°N, 12.28°E	49.9	91–94, 96	6029
D	Grado Lagoon	Valle Artalina	45.41°N, 13.26°E	79.8	90–94	275
E	Po river course	Ficarolo, Ravalle	44.55°N, 11.30°E	90.0	90–91, 93–95	136
F	Comacchio Lagoon	Lavadena, Valle Campo, Saline	44.38°N, 12.12°E	95.5	90–94, 96	940
G	Cervia Saline	Cervia Saline	44.16°N, 12.19°E	132.9	90–97	324
H	Margherita di Savoia	Margherita di S. Saline	41.24°N, 16.03°E	528.5	93–97	729

Survival probability was estimated by maximum likelihood from individual encounter histories (Table 2, Lebreton et al. 1993). This parameter, noted Φ, should be seen as the product between the local survival probability and a movement probability. Φ has a slightly different meaning according to the age of the bird. In birds captured at the moulting site, the parameter Φ is 'the probability of surviving and using the moulting site at least once again in their life', while for birds ringed earlier as chicks this corresponds to 'the probability of surviving and reaching this moulting site'. The parameter Φ is generally referred to as local survival because permanent emigration, i.e. birds never recaptured after marking, would be confounded with mortality, i.e. the complement of Φ to 1. We will refer to Φ as "survival/movement" to remind the reader of its two components. Evidence about site fidelity, the probability of not visiting the moulting site, can potentially be derived by the estimate of the probability of recapture, noted "p". Individuals using the moulting site on a regular basis would have a higher probability of recapture (Viallefont et al. 1995). No recaptures were made during breeding, and as a consequence, recapture probability at the colonies were fixed to 0.00 (Table 2 and Fig. 2). Note that for each year we considered two occasions but the capture probability could be estimated only in one. As a consequence, the parameter we modelled, Φ, is the square root of the annual survival.

Modelling survival/site-fidelity and recapture probability

Model selection started from the model (Φ_l' Φ_l; p_t' p_t) assuming that the survival/movement parameter depended on age and breeding location, noted "l". In model notation, Φ′ refers to juveniles and Φ to adults. We also used the distance on logarithmic scale, noted "d", between the birth colony and the moulting site as a predictor of Φ′. The recapture probability was assumed to vary according to age (p′ refers to juveniles and p to adults) and year, noted "t", but no interaction was considered between these two effects given the sparseness of data. The goodness of fit of this model was estimated using the bootstrap procedure on 300 simulated data sets (White and Burham 1999). A significant test would indicate a large extra-multinomial variance. In this case the model deviance should be corrected using a variance inflator factor, ĉ (Lebreton et al. 1992). The model selection procedure followed the modified Akaike Information Criterion (QAICc; Burnham and Anderson 1998). The model with the lowest QAICc can be considered as the best compromise between the model deviance and the number of parameters in the model. In the presence of extra-multinomial variation, the QAICc value is calculated by dividing model deviance by ĉ,

Table 2. Types of capture-histories in the data set. The three capture-histories in the example are related to individuals released in year i and caught at every subsequent capture-recapture occasion. C = captured and released at the colony. M = captured and released at the moulting site (note that during C-occasions no adults were marked and/or already marked birds were captured).

Year	i		i+1		i+2	
Occasion	C	M	C	M	C	M
Adult	0	1	0	1	0	1
Yearling	0	1	0	1	0	1
Yearling	1	1	0	1	0	1

where ĉ is the variance inflator factor (Anderson and Burnham 1999). The significance of specific effects can also be investigated using a χ^2-test between two models, provided they are nested (Lebreton et al.1992). Note that when extra-multinomial variation is present an F-test could be used instead, however, when ĉ is estimated by bootstrap, the F-test is asymptotically equivalent to a χ^2 when effective sample size is large (G. White pers. comm.). Models were built and fitted to the data using software MARK1.9 (White and Burnham 1999). Models with similar QAICc values, i.e. within 4–7 points, should be considered (Burnham and Anderson 1998). To incorporate model uncertainty for parameter estimation, estimates were obtained by averaging those of all models weighed for the relative importance of their QAICc values (Burnham and Anderson 1998 for more details). Finally, the likelihood optimisation function might not converge properly on sparse datasets (due to the presence of local minima), giving a biased estimate of the parameters. To avoid this problem all models were run more than once using different starting values for the function.

Results

We analysed a total of 12,185 encounter histories of which 72% referred to birds that had been ringed as chicks. Despite this large initial number of individuals, little information was available to estimate recapture and local survival probabilities as only 3.7% of the marked birds were recaptured. The goodness of fit of the initial model (Φ_l' Φ_l; p_t' p_t) indicated the presence of extra-multinomial variation and a variance inflation factor was used to correct model deviance ($\hat{c} = 1.37$). As expected, estimates of recapture probability were generally low and varied significantly according to both year and age ($\chi^2_7 = 17.18$, $P = 0.016$ and $\chi^2_1 = 38.80$, $P = 0.001$, respectively; Fig. 3). Juveniles were more likely to be recaptured than adults. The survival/movement parameter varied according to the location of the colony of birth in juveniles ($\Phi_l'\Phi_l$ $p_t'p_t$ vs $\Phi_.'\Phi_l$ $p_t'p_t$: $\chi^2_6 = 29.17$, $P = 0.001$), but not in older individuals ($\Phi_l'\Phi_l$ $p_t'p_t$ vs $\Phi'.\Phi_l$ $p_t'p_t$: $\chi^2_7 = 5.08$, $P = 0.651$). Similarly, adult survival was not affected by whether the bird had been ringed as a chick in previous years, or as adult/juvenile at the moulting site ($\Phi_l'\Phi.$ $p_t'p_t$ vs Φ_l' Φ^3_l $p_t'p_t$: $\chi^2_1 = 2.37$, $P = 0.124$). The model Φ_l' Φ; p_t' p_t must be viewed as the best compromise between parameters and model deviance as suggested by its low QAICc value (Table 3). A further reduction in QAICc value was obtained when the influence of the location of birth was modelled as a function of the distance expressed on a logarithm scale (model Φ_d' Φ; p_t' p_t; Table 3). Having corrected for colony distance, little variation was left to be explained by colony characteristics other than its distance from the moulting site. Indeed colony distance explained 90.5% of the between-colony variation. This can be calculated by the ratio of the deviance explained by model Φ_d' $\Phi.$; p_t' p_t and the total between colony variation (difference in deviances between model Φ_l' $\Phi.$; p_t' p_t and $\Phi_.'$ $\Phi.$; p_t' p_t = 33.754/37.296 = 0.905). This suggests that in the first 2–4 months of life, the average survival/movement of birds hatched at different locations mainly differed by a multiplicative factor that was a function of the distance. Hence, we fitted the same model using a logarithm link function (model Φ_d' $\Phi.$; p_t' p_t^1; Table 3) so that the relation between Φ' and the multiplicative factor would be linear (Viallefont 1995). Although this model had a similar QAICc value, it was preferred to the previous one given the multiplicative relation of its two components (the survival probability and the probability, conditional on survival, of reaching the site). The suggested relationship was:

$$\Phi' = e^{2.237 - 0.837 \cdot (d)}$$

where d is the logarithm of the distance from the moulting site expressed in km (Fig. 4).

We should note that the model Φ_d' Φ_d; p_t' p_t has the lowest value of QAICc (Table 3). This model assumes an effect of colony distance even for adults. Despite the lowest QAICc value, this model has not been considered further. Adding an extra parameter to a model, in this case Φ_d' $\Phi.$; p_t' p_t^1, would always result in a decrease in deviance. For a non-significant effect, i.e. $\chi^2_1 < 3.84$, the resulting QAICc value would always be between +2 and −1.84 of the previous model. Hence the effect of distance on adults should be seen as not significant

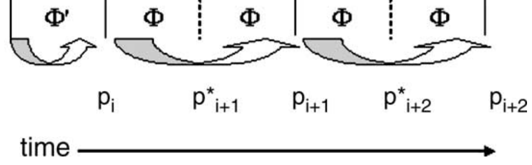

Fig. 2. Schematic representation of the parameters Φ and p over time. C = marked at the colony (only fledglings). M = captured and released at the moulting site. Recapture probability at the colony, noted p*, is 0.

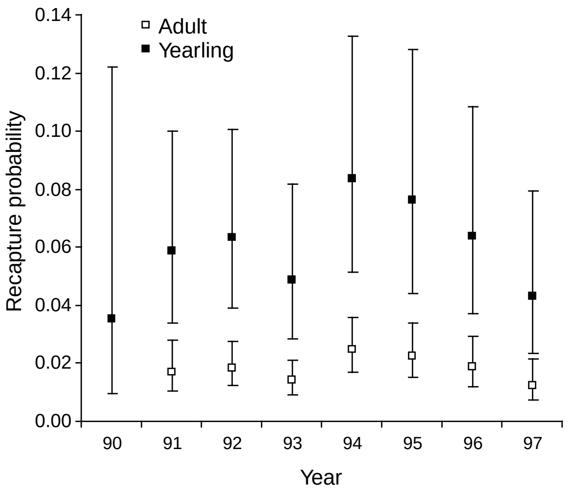

Fig. 3. Recapture probability of adult and juvenile little terns from model ($\Phi'_l\ \Phi_l;\ p'_t\ p_t$). The model assumes an additive effect of age. Bars indicate 95% confidence intervals. Note that the Y-axis is cut at 0.14.

even if the model had the lowest QAICc. Such uncertainty is however taken into consideration in parameter estimates by the averaging technique. Model $\Phi'_d\ \Phi.;\ p'_t\ p_t$[1] was thus retained as the best compromise between the model deviance and the number of parameters in the model (Table 3). A significant inverse relationship with distance still held, even when the most distant colony, colony H (Fig. 4), was not considered (results not shown). A second model assuming a quadratic relationship of the type $\Phi' = e^{a+b\cdot(d)+c\cdot(d2)}$ had a similar fit to the one of the retained model (Table 3) but included an additional parameter. A model assuming a linear relationship with distance of the type $\Phi' = a + b\cdot(d)$ was not retained. Finally, when the effects of age and year were re-tested on the probability of recapture maintaining the retained structure on survival (model $\Phi'_d\ \Phi.;\ p'_.\ p_.$ and model $\Phi'_d\ \Phi.;\ p_t$), they still proved to be significant (results not shown). Model selection ended with a few models within a small range of QAICc values. The average estimate of adult survival throughout all models was 0.948 (95% confidence interval between 0.874 and 0.980), which corresponds to a yearly survival of 0.899 (0.963–0.836; confidence intervals calculated using the δ-methods, Morgan 2000). This constant value gives an average life-time expectancy of about 9.39 years from maturity. The value 0.601 (95% confidence interval between 0.287 and 0.850) estimated for the closest location (B, Fig. 4) is probably near to the real juvenile survival of little tern between fledging (peak: late June) and the pre-migratory stay at the moulting site (peak: late August). An idea of the first-year survival can be obtained by the product 0.601 · 0.948 (0.578; 0.737–0.418).

Discussion

Model hypotheses

The main interest of this analysis was to model the influence of age, colony of birth and distance from colony on the survival/movement parameter estimated

Table 3. Modelling effects influencing the survival/movement and recapture probabilities of little terns at the moulting site. Model notation (see also text): Φ' = survival/movement parameter for juveniles; Φ = survival/movement parameter for adults; p' = probability of recapture for a juvenile; p = probability of recapture for an adult; l = location of birth, d = logarithm of the distance between location of birth and moulting site; t = year effect. Note that no interaction term between age and year effect on the probability of recapture was included. ΔQAICc = difference between the model QAICc and the one with the lowest value. np = number of estimable parameters in the model. QAICc weight = the relative importance of each model. The sum of all QAICc weights is 1.

Model	QAICc	ΔQAICc	QAICc weight	np	QDeviance
$\Phi'_d\ \Phi_d;\ p'_t\ p_t$	3831.18	0	0.34	13	219.60
$\Phi'_d\ \Phi.;\ p'_t\ p_t$	3831.50	0.32	0.29	12	221.93
$\Phi'_d\ \Phi.;\ p'_t\ p_t$ [1]	3832.03	0.85	0.22	12	222.45
Φ_{d+d}[2] $\Phi.;\ p'_t\ p_t$	3833.50	2.31	0.11	13	221.92
$\Phi'_d\ \Phi.;\ p'_t\ p_2t$	3837.31	6.12	0.02	12	227.73
$\Phi'_l\ \Phi_l$[3]; $p'_t\ p_t$	3837.63	6.45	0.01	18	216.03
$\Phi'_l\ \Phi.;\ p'_t\ p_t$	3838.00	6.81	0.01	17	218.40
$\Phi'_l\ \Phi_l;\ p'_t\ p_t$	3839.80	8.62	0.00	18	218.20
$\Phi'_l\ \Phi_l;\ p'_t\ p_t$	3846.97	15.78	0.00	24	213.32
$\Phi'_l\ \Phi_l;\ p'_.\ p.$	3850.10	18.92	0.00	17	230.50
$\Phi'_.\ \Phi.;\ p'_t\ p_t$	3863.25	32.07	0.00	11	255.68
$\Phi'_.\ \Phi_l;\ p'_t\ p_t$	3864.09	32.91	0.00	18	242.48
$\Phi'_l\ \Phi_l;\ p_t$	3883.76	52.57	0.00	23	252.11

[1] Model with log-link function.
[2] Model with identity-link function.
[3] Two adult survival/movement parameters, one for the birds marked at the moulting site and the other for the birds marked on the breeding colonies.

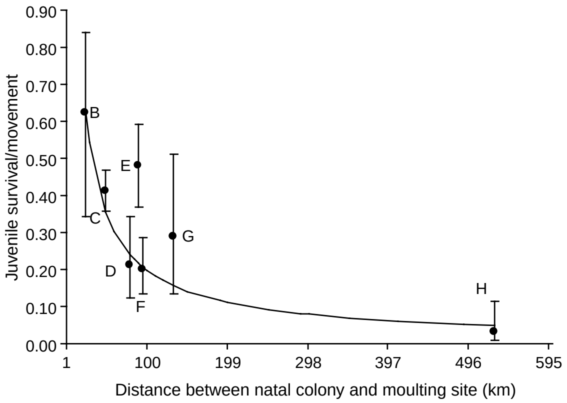

Fig. 4. Juvenile survival at the moulting site as a function of the distance from the location of birth. A log-link function was used in the model ($\Phi'_d \; \Phi.$; $p'_t \; p_t{}^1$; Table 3).

at the moulting site. Most individuals were recaptured only once. This scarce information has inevitably restricted the number of effects that could be controlled for to those based on a priori hypotheses (Anderson and Burnham 1999). The choice of these hypotheses, and not of others, deserves a short discussion. First, we considered two age classes only (but see below). All birds older than about 5 months were considered homogeneous with regard to survival and recapture parameters. This is unlikely, but full age-dependent models would have clearly contained too many parameters. In long-lived vertebrates, survival generally increases steadily in the first age classes and subsequently levels off before it possibly starts to decline in very old age. In a capture-recapture framework, large sample sizes and/or high probability of recapture are needed to describe such a pattern (Tavecchia et al. 2000, see also examples in Nur and Sydeman 1999, Fredericksen and Bregnballe 2000). Second, although we considered a year effect in the probability of recapture, the same has not been done for the local survival/movement parameter. This seems disputable because the number of terns caught at the moulting site declined in the last years of the study. This decline could be due to a decrease in survival/movement probability, i.e. higher mortality/permanent emigration, and/or to a decrease in capture probability. The probability of recapture did apparently decrease in the last three years of the study, but we were not able to test such a variation for the survival/movement pattern properly. Information on adults was too sparse to account for such a trend. The overall sample size was large for juveniles, but the irregular use of the breeding sites would have allowed only few year-by-colony comparisons and no chance to correct for both simultaneously. Thus, we rather opted to fully investigate the influence of the location of birth. Finally, although we considered the statistical interaction between age and colony in the local survival/movement parameter, the relation between age and time in the probability of recapture was assumed to be additive. This is not a strong assumption as the estimate of survival parameters should be robust as regards the structure in the probability of recapture.

Pre-migratory movements and demography of little terns

We estimated a parameter that included the survival probability and the probability, conditional on survival, of reaching or re-visiting the moulting site. The average yearly local survival/movement parameter for adults was 0.899, a value very similar to the survival estimate found for other species of terns (Spendelow et al. 1995, del Hoyo et al. 1996). This suggests that adults are very likely to come back to the same moulting site. However, they had a lower probability of recapture compared to juveniles. This might be due to different reasons, one being simply that adults roost at sea, or have a greater skill in avoiding the nets by adults. Another is that this value, averaged over age, is affected by age-specific use of the moulting site. Gaps in site attendance would have the effect of a temporary emigration and negatively affect the probability of recapture. In lesser snow geese *Anser caerulescens caerulescens*, individuals skipping reproduction have a lower probability of recapture at the breeding site (Viallefont et al. 1995). Similarly Pugesek and Diem (1990) concluded that the lower recapture probability of young Californian gulls *Larus californicus* was due to an increased access to reproduction with age. For a similar reason, females had a higher probability of skipping reproduction (Pugesek et al. 1995). In our case, the pattern shown by adult little terns most probably reflected an age-dependent use of the site, with birds in their second summer-assigned to the 'adult' category-scarcely visiting the moulting site. Indeed, little terns reach sexual maturity when 2–3 years old and a large fraction of one-year birds remain on the wintering grounds (Cramp 1985). This is strongly suggested by a previous analysis, conditional on recapture at the same roosting site, in which only 5.6–5.9% of the birds caught was made up by one-year terns (Cherubini et al. 1996), despite that we found that young individuals have higher probability of recapture. We did not have enough data to include a third age class, i.e. one-year old, from the start, but we included it in an *ad hoc* model built from the retained one in order to test the above hypotheses. Results were not conclusive in this respect (not shown). The probability of recapture of one-year old terns was virtually zero (ranging from 0.0042 to 0.0079), but the one of adults was still significantly lower then the one of juveniles.

In birds marked as fledglings and recaptured a few months later, the survival/movement parameter was estimated as the product between the survival probability in the first 2–4 months of life and the probability of using the moulting site. This parameter changed significantly according to birth location, being negatively related to the distance from the moulting site. The most likely explanation is that distance affected the movement probability rather than the survival probability. Although we cannot separate the role of the two factors, there is no reason to consider that survival decreases strongly with the distance from the moulting site. For a long-distance migrant, a post-breeding dispersal of few hundred km, in the absence of ecological and physical barriers and in a climatically mild season, does not seem to represent an important source of mortality. Thus, if the variation in local survival was mainly due to the probability of reaching the site, the average survival from fledging to migration should approximately correspond, for all colonies, to the value estimated at the closest breeding location (0.601). This seems to be supported by the fact that the model, assuming a negative correlation with the colony-moulting site distance, explained more than 90% of the difference on local survival between locations and very little was left that could be explained by a breeding location effect alone. In contrast, the survival/movement parameter of adults was not influenced by the natal colony location, even when the colony effect was replaced by the colony-to-moulting site distance. This suggests that individuals that have visited the moulting site at least once tend to visit it again with a similarly high probability regardless of the location of birth. Given that juveniles are still accompanied by adults when they arrive at the moulting site, low probabilities for juveniles that reach it from the farthest colonies are probably paired to equally low numbers of adults which breed there and faithfully re-visit the moulting site. This scenario could hold true in all three possible settling behaviours of breeding adults, i.e. phylopatry, breeding site fidelity, or frequent redistribution of breeders within a large area. Fixation upon the moulting site would probably be achieved by the first time they visit it (when juvenile), consistent with the general mechanism of site fixation (Ketterson and Nolan 1990). The existence of one or more similar moulting sites probably in the southern Adriatic Sea has to be postulated in order to account for the large fraction of southern birds that did not turn up at the Venice moulting site.

Conservation issues

The Mediterranean is generally considered an oligotrophic sea (Margalef 1985). Such a low level of resources has been ascribed to relative deep waters and weak currents. Nevertheless, highly productive spots are found in connection with the run-off of big rivers and areas of wind mixing (Lloret et al. 2003). The northern Adriatic Sea is a particularly productive area, due to the large fresh-water input by the Po and other rivers, combined with the mixing effect caused by strong winds and tidal movements. Tides, in particular, reach remarkable amplitudes for the Mediterranean standards here. In addition, large coastal lagoons with shallow waters seasonally attract large amounts of juvenile stages of catadromous fish as well as small-sized marine species (Ardizzone et al. 1988). These general features probably create large trophic resources for little terns and, together with other ecological and physical conditions, make the Lagoon of Venice an important destination of moult migration. The existence of large post-breeding gatherings in other parts of the species range (e.g. on the Dutch coast and in the Nile Delta; Meininger et al. 1987, Goodman and Meininger 1989, Keijl and Koopman 1991) suggests that moult migration is a widespread behaviour among little tern populations. A ‘catchment’ range of 500 km was shown for the Venice moulting site, but other similar sites attract the majority of birds originating from the southern area of the Adriatic Sea. The 500 km range cannot be postulated for other moulting sites as this probably varies at a great extent according to the local availability and distribution of alternative sites. Patches of rich waters coupled with coastal lagoons have been found along the south-eastern coasts of the Adriatic Sea. Combining our estimates, nearly 41% of the fledglings are expected to moult elsewhere (results not shown). Given the number of fledglings marked from 1990 to 1997 this value corresponds to a minimum of 2,200 birds over the 8 year period. Whether any of these sites are used as moulting areas by little terns, and especially by individuals coming from the Italian colonies, is unknown. However, post-breeding gatherings have been reported along the coast of Albania (T. Bino pers. comm.) and northern Greece (A. Bonetti pers. comm.). Knowledge and protection of the moulting sites all over the species range-in view of their role of as ‘population funnels’-would allow the development of a full conservation strategy for the breeding populations.

Acknowledgements – Many thanks to Roger Pradel for helping with data analysis. Fabrizio Sergio, Daniel Oro and Iris Hendriks provided useful comments on an early version of the manuscript. We are indebted to the ringers who marked chicks at the colonies and to members of the ‘Anonima Limicoli’ who caught birds at the moulting site. Morten Frederiksen and an anonymous referee provided useful comments and ideas.

References

Anderson, D. R. and Burnham, K. P. 1999. General strategies for the analysis of ringing data. – Bird Study 46: 261–270.

Archibald, G. and Landfried, S. 1993. Conservation measures for the Siberian crane. – In: Moser, M. and van Vessem, J. (eds). Wetland and waterfowl conservation in south and west Asia. IWRB Special Publ. 25: 85–87.

Ardizzone, G. D., Cataudella, S. and Rossi, R. 1988. Management of coastal lagoon fisheries and aquaculture in Italy. – FAO Fish Tech. Pap. 293: 103 pp.

Boere, G. C. 1976. The significance of the Dutch Waddenzee in the annual life cycles of arctic, subarctic and boreal waders. Part I. The function as a moulting area. – Ardea 64: 210–291.

Bourdeau, Ph., Martin, J.-M., Mei, C. C., Musu, I., Vellinga, P. and Beinat, E. 1998. Report on the mobile gates project for the tidal flow regulation at the Venice Lagoon inlets. – Quaderni Trimestrali Consorzio Venezia Nuova, 6, suppl.:57–106.

Burnham, K. P. and Anderson, D. R. 1998. Model selection and inference. A practical information – theoretical approach. – Springer–Verlag, New York.

Cherubini, G., Serra, L. and Baccetti, N. 1996. Primary moult, body mass and moult migration of little tern *Sterna albifrons* in NE Italy. – Ardea 84: 99–114.

Cramp, S. (ed.). 1985. The birds of western Paleartic. Vol. V. – Oxford University Press.

del Hoyo, J., Elliott, A. and Sargatal, J. 1996. Handbook of the birds of the World. Vol 3. Hoatzin to Auks. – Lynx Edicions, Barcelona.

des Clers B. 1976. Proposals for flyway management. – In: Smart M. (ed.) Proceedings of the international conference on the conservation of wetlands and waterfowl, Heiligenhafen 1974, p. 449–458.

Evans, P. R., Davidson, N. C., Piesma, T. and Pienkoski, M. W. 1991. Implications of habitat loss at migration staging posts for shorebird populations. – Acta XX Congr. Int. Ornithol, pp. 2228–2235.

Fasola, M., Saino, N., Canova, L. and Bogliani, G. 1989. Breeding and summering populations of gulls and terns in coastal wetlands on the Adriatic Sea. – Le Gerfaut 79: 177–184.

Fasola, M., Sanchez Guzman, J. M. and Roselaar, C. S. 2002. *Sterna albifrons* little tern. – BWP Update 4: 89–114.

Frederiksen, M, Fox, A. D., Madsen, J. and Colhoun, K. 2001. Estimating the total number of birds using a staging site. – J. Wild. Manage. 65: 282–289.

Gauthier, G., Pradel, R., Menu, S. and Lebreton, J.-D. 2001. Seasonal survival of greater snow geese and effect of hunting under dependence in sighting probability. – Ecology 82: 3105–3119.

Goodman, S. M. and Meininger, P. L. (eds). 1989. The birds of Egypt. – Oxford University Press, Oxford.

Hedenström, A. and Sunada, S. 1999. On the aerodynamics of moult gaps in birds. – J. Exp. Biol. 202: 67–76.

Hötker, H. and Frederiksen, M. 2001. Estimation of total numbers of pied avocets *Recurvirostra avosetta* using a moulting site in the Danish Wadden Sea. – Ardea 89: 537–541.

Jehl, J. R. Jr. 1988. Biology of the eared grebe and Wilson's phalarope in the non–breeding season: a study of adaptations to saline lakes, Stud. Avian Biol. No. 12, 144 pp.

Jehl, J. R. Jr. 1990. Aspects of the moult migration. – In: Gwinner, E. (ed.). Bird migration. Springer Verlag, Berlin, pp. 102–113.

Keijl, G. and Koopman, E. V. 1991. Veel Aalscholvers *Phalacrocorax carbo* en Dwergstern *Sterna albifrons* op Rottumeroog, in juli en augustus 1990. – Sula 5: 146–149.

Ketterson, E. D. and Nolan, V. Jr. 1990. Site attachment and site fidelity in migratory birds: experimental evidence from the field and analogies from neurobiology. – In: Gwinner, E. (ed.). Bird migration. Springer Verlag, Berlin, pp. 117–129.

Lebreton, J.-D., Burnham, K. P., Clobert, J. and Anderson, D. R. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. – Ecol. Monogr. 62: 67–118.

Lebreton, J.-D., Pradel, R. and Clobert, J. 1993. The statistical analysis of survival in animal populations. – Trends Ecol. Evol. 8: 91–95.

Lloret, J., Palomera, I., Salat, J. and Sole, I. 2003. Impact of freshwater input and wind on landings of anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) in shelf waters surrounding the Ebro River delta (northwestern Mediterranean). Fishery Oceanography in press.

Madsen, J. 1996. International action plan for the lesser white–fronted goose (*Anser erythropus*). – In: Heredia, B., Rose, L. and Painter, M. (eds). Globally threatened birds in Europe. Council of Europe Publishing.

Margalef, R. 1985. Introduction to the Mediterranean. – In: Margalef, R. (ed.). Key environments: western Mediterranean. London, Pergamon Press.

Meininger, P. L., van Swelm, N. D. and Swennen, C. 1987. Biometrie, rui en herkomst van Dwergsterns *Sterna albifrons* in het Deltagebied. – Limosa 60: 75–83.

Morgan, B. J. T. 2000. Applied stochastic modelling. – Arnolds Text in Statistics, London.

Murphy, M. E. 1996. Energetics and nutrition of molt. – In: Carey, C. (ed.). Avian energetics and nutritional ecology. Chapman Hall, New York, pp. 158–198.

Muselet, D. 1985. Les quartiers d'hivernage des sternes naines européennes *Sterna albifrons*, L'Oiseau et la Revue Francaise d. – Ornithologie 55: 183–193.

Muselet, D. 1997. Little tern *Sterna albifrons*. – In: Hagemeijer, W. J. M. and Blair, M. J. (eds). The EBCC atlas of European breeding birds: their distribution and abundance T&AD Poyser, London.

Nur, N. and Sydeman, J. 1999. Survival, breeding probability and reproductive success in relation to population dynamics of Brandt's cormorants *Phalacrocorax penicillatus*. – Bird Study (suppl.) 46: 92–103.

Pirazzoli, P. A. 2002. Did the Italian government approve an obsolete project to save Venice? – Eos 83: 217–223.

Pugesek, B. H. and Diem, K. L. 1990. The relationship between reproduction and survival in known–aged California gulls. – Ecology 71: 811–817.

Pugesek, B. H., Nations, C., Diem, K. L. and Pradel, R. 1995. Mark–resighting analysis of California gull population. – J. Appl. Stat. 22: 625–639.

Ravera, O. 2000. The Lagoon of Venice: the result of both natural factors and human influence. – J. Limnol. 59: 19–30.

Salomonsen, F. 1968. The moult migration. – Wildfowl 19: 5–24.

Schaub, M. and Jenni, L. 2001. Variation of fuelling rates among sites, days and individuals in migrating passerines birds. – Funct. Ecol. 15: 584–594.

Serra, L. 1993. Juvenile little terns starting primary moult in Europe. – Ring. Migr. 14: 148.

Smit, C. J. and Piersma, T. 1989. Numbers, midwinter distribution, and migration of wader populations using the East Atlantic flyway. – In: Boyd, H and Pirot, J. Y. (eds). "Flyways and reserve networks for water birds". IWRB Spec. Publ. 9: 24-63.

Spendelow, J. A., Nichols, J. D., Nisbet, I. C. T., Hays, H., Cormons, G. D., Burger, J., Safina, C., Hines, J. E. and Gochfeld, M. 1995. Estimating annual survival and movement rates of adults within a metapopulation of roseate terns. – Ecology 76: 2415–2428.

Swaddle, J. P. and Witter, M. S. 1997. The effects of molt on the flight performance, body mass, and behavior of European starlings (*Sturnus vulgaris*): an experimental approach. – Can. J. Zool. 75: 1135–1146.

Swaddle, J. P., Witter, M. S., Cuthill, I. C., Budden, A. and McCowen, P. 1996. Plumage condition affects flight performance in common starlings: implications for developmental homeostasis, abrasion and moult. – J. Avian Biol. 27: 103–111.

Szijj, J. 1972. Some suggested criteria for determining the international importance of wetlands in the Western Palaearctic. – In: Carp E. (ed.). Proc. Int. Conf. on Wetlands and Waterfowl, Ramsar, Iran. IWRB, pp. 111–124.

Tavecchia, G., Pradel, R., Boy, V., Johnson, A. and Cézilly, F. 2000. Sex- and age-related variation in survival probability and the cost of the first reproduction in breeding greater flamingos. – Ecology 82: 165–174.

Viallefont, A. 1995. Robustesse et flexibilité des anlyses démographiques par capture-recapture: de l'estimation de la survie à la detection de compromis évolutifs. – Ph.D. Thesis, Université de Montpellier II.

Viallefont, A., Cooke, F. and Lebreton, J.-D. 1995. Age-specific costs of first-time breeding. – Auk 112: 67–76.

White, G. C. and Burnham, K. P. 1999. Program MARK: survival estimation from populations of marked animals. – Bird Study 46 (suppl.): 120–129. [http://www.cnr.colostate.edu/ gwhite/software.html].

(*Received 13 April 2004, revised 8 September 2004, accepted 21 October 2004.*)