PRIMARY MOULT, BODY MASS AND MOULT MIGRATION OF LITTLE TERN STERNA ALBIFRONS IN NE ITALY

GIUSEPPE CHERUBINI, LORENZO SERRA & NICOLA BACCETTI


Large post-breeding gatherings of Little Terns Sterna albifrons are regularly observed in the Lagoon of Venice, Italy. Here, during five consecutive trapping seasons, 2956 birds were examined and ringed. Their breeding area, as indicated by 163 direct recoveries (mainly juveniles, ringed as chicks), spans over a broad sector of the Adriatic coasts, with colonies located up to 133 km far. During their stay at the study area, adults undergo an almost complete moult. Two partial primary moult cycles can be observed, the first of them being suspended when 2-4 outermost long primaries have not yet been shed. Pre-migratory body mass build-up, enough for a flight longer than 1000 km, takes place during the very last days before departure to the winter quarters, in most cases when the moult has reached a suspended stage. Active primary moult and body mass increase do overlap in late moulting birds (after 27 August), indicating that the two processes are compatible, in case of time shortage. Post-breeding movements to the Lagoon of Venice seem to fit most requisites of moult migration.

Key words: Sterna albifrons - Italy - biometrics - moult migration - ringing - fattening

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INTRODUCTION

Beside other energy demanding processes such as migration and breeding, moult is one of the most critical functions in the annual life cycle of birds (Murton & Westwood 1977; Blem 1980; King 1980; Walsberg 1983; Blem 1990). Most species tend not to overlap these events (Payne 1972; King 1974; Hale 1980), although feather production and pre-migratory body mass build-up are considered compatible in many cases (Koopman 1986; Jehl 1988; Lovvorn & Barzen 1988; Zwarts et al. 1990; Holmgren et al. 1993a; Piersma & Jukema 1993). Wing moult, apart from consuming energy for the growth of new feathers, reduces or even prevents the flight capability and increases the energetic cost of flight and the risk of predation (Smit & Piersma 1989; Holmgren et al. 1993b).

Many species which shed remiges simultaneously (Podicipedidae, Phoenicopteridae, Anatidae, Gruidae, Alcidae) perform moult migrations, gathering to moult in particular areas where food supply is abundant and flightless birds safe from predators (Salomonsen 1968; Jehl 1990). Indications of moult migration have also been found in a few species (some Charadriidae, Scolopacidae and Passeriformes) that do not undergo a synchronous wing moult (Boere 1976; Jehl 1990; Thompson 1991). Food abundance in the moultting areas is probably the main cause for the development of moult migration in these cases (Jehl 1987; Rohwer & Manning 1990; Thompson 1991; Young 1991). The features of moult migration described so far are: (a) flight-feathers are replaced in special areas, distinct from breeding and wintering grounds; (b) moult migratory direction does not have to coincide to that of autumn mi-
igration; (c) some age or sex classes may not perform it; (d) moulting areas are very localised; and (e) high numbers of individuals are involved (Salomonsen 1968; Jehl 1990).

Outside the breeding season, the Little Tern Sterna albifrons is one of the least known terns of the Palearctic. Migration routes and even the location of winter quarters are not well known (Luchrs & Rittinghaus 1974; Clancey 1981; Muselet 1985; Wymenga & Altenburg 1992). Moulting strategy and biometrics have been described only from very localised situations and relatively small numbers of birds (Nadler 1978; Clancey 1981; Streichert 1982; Meiningher et al. 1987; Muselet 1988). Finally, little information is available on pre-migratory dispersal following the breeding season and formation of communal roosts (Keijl & Koopman 1991), though the European Little Tern is generally considered less gregarious than its American counterpart, the Least Tern Sterna antillarum and most other Sterna species (cf. Glutz von Blotzheim & Bauer 1982; Cramp 1985).

Italy held 30% of the western Palearctic population of Little Tern (Fasola 1986a; 1986b); 6000 pairs were censused during 1983 and 1984 breeding seasons. A dramatic population decrease has recently been recorded at some of the main colonies (Fasola et al. 1993; M. Passarella pers. comm.). At a nocturnal roosting site, where the largest known flocks had been observed (up to 7000 birds in August), we have been carrying out a regular ringing programme over 5 years. Basing on a sample of 2956 birds caught thus far, in this paper we aim to analyse (1) numbers, origin and phenology of birds visiting the roost; (2) the existence and timing of a pre-migratory body mass increase; (3) the wing moulting strategy of adult birds, between the end of the breeding season and departure towards the winter quarters, and the moulting condition of individual birds examined in different years; and (4) the temporal relationships between wing moulting and body mass variation. Finally, whether such high post-breeding concentrations of Little Terns can be explained as a consequence of moult migration is discussed.

**STUDY AREA**

Over 80% of the Italian population of the Little Tern breeds along the north-western Adriatic coast, where more than 1000 km² of estuarine habitat is available. The Lagoon of Venice (45°11′N-45°35′N, 12°07′E-12°38′E) is located in the middle of this wetland system and represents 50% of its total surface area. It is in free connection with the Adriatic Sea, except a peripheral sector (90 km²) which was dammed in order to improve a traditional form of fish-farming ('vallicoltura'). The tidal part of the lagoon mostly includes shallow water (depth 0-1.5 m at low tide), mudflats, salt-marshes and some deeper canals; the average tidal range is 90 cm. Sandy beaches occur only on the neighbouring seashore and at a single tidal sand-bar ('Bacan') in the northern part of the lagoon, where the high-tide roost of the terns was located.

The lagoon itself is indeed less important for breeding Little Tern than its size may suggest: 500 pairs were present during Fasola's (1986b) survey and a sharp decrease has been recorded in more recent years, as 200 pairs bred in 1990 and no more than 100 pairs in 1991 and 1992 (Scarton et al. 1994). Although the roosting site was never successfully used for breeding in 1990-94, it regularly held more than 5000 and up to 7000 Little Terns per night between mid-July and early September each year (Serra et al. 1992). Smaller numbers of Black Terns Chlidonias niger also occurred. During the breeding season (May and June), as well as after the beginning of September, only up to a few hundred Little Terns were observed; none were recorded in winter. The roost lies on the only sand-bar of the lagoon which is not submerged by average spring tides; it was never formed during diurnal high tide, the terns gathering by the water edge at sunset, regardless of the time of the next high tide. The flock steadily moved toward the centre of the sand-bar as the tide rose. The distance between the roost and the main Italian breeding colonies (e.g. Po Delta, Comacchio Lagoon, Cervia Salines) is 60-133 km (Fig. 1).
METHODS

Little Terns were trapped from May to September 1990-94, as a part of a ringing programme carried out year-round. A total of 150-300 m of mist-nets was set up before sunset near the roosting site in one or two consecutive catching nights during spring tide periods (every two weeks). The nets (single panels, height 80 cm, mesh 30 mm, monofilament nylon thread) were checked at hourly intervals during the first 1-3 h after sunset and then removed.

Body mass of birds was recorded between 2 and 6 h after sunset, with an electronic Sartorius balance (accuracy 0.1 g). No correction indices were applied, as the analysis of hourly samples gave highly variable indications of mass loss on different nights, not significant in most cases. Wing length (max. chord) was measured to the nearest mm, bill length (tip to feathering) to the nearest 0.1 mm. Data from the five years were pooled and arranged into a series of standard 7-day periods, numbered from the beginning of the year (Berthold 1973) and running from 21-27 May (period 21) to 17-23 September (period 38). Only primary moult of adults was analysed, although both adults and juveniles underwent a complete body moult and adults renewed all tertials, part of secondaries and almost all rectrices. Although some juveniles shed one or two primaries before leaving towards the winter quarters (Serra 1993), the moult pattern in this age class was not considered for analysis because of the rarity of moulting birds (30 out of 373 in 1993 and 1994). Second-year birds, identified by plumage characters (number of dark outer primaries) and confirmed by 12 ring controls, were excluded from moult analysis too.

The primary moult was described using the following parameters: (1) primary score: each feather was scored on a scale from 0 to 5 (Ginn & Melville 1983) and these scores summed. As two moult series may be active together, to score the advanced stages of the first moult series we considered as score 5 all the primaries shed for the second time; (2) number of shed feathers of the first moult series; (3) number of growing feathers of both series; and (4) raggedness score (RS) of both series. The score of each growing feather was subtracted from the score of a full-grown fe-
ather and these scores were summed (cf. Holmgren et al. 1993b). Possible year-to-year differences in the timing of primary moult were searched for, confronting moult scores of individual adult birds captured in two different years between periods 28 (9-15 July) and 37 (10-16 September). These differences had to be corrected for the influence of the temporal gap between weeks of ringing and retrap. The correction factors were obtained from a linear regression formula of moult score differences on distance between ringing and retrap expressed in number of weeks (expected moult score difference = 2.816 * week distance + 0.187; \( r = 0.83, F_{1,38} = 84, P < 0.001 \)). Only post-breeding periods with a sample size larger than 15 individuals for each age class (28-36) were considered for analysis. The absence of a significant pattern of variation in wing and bill lengths of adults trapped in different periods (weekly means ranging 174.0-175.7 mm for wing and 30.3-30.7 mm for bill) leads us to analyse body mass independently from body size, apart from the case of multiple regression. Body mass values were \( \log_{10} \) transformed for normality. Multiple regression, stepwise selection method, probability of \( F \) to enter 0.01, was run testing transformed body mass values as dependent variable on moult score, number of shed feathers, number of growing feathers, raggedness score, wing-length and 7-day period as independent variables. Statistic analysis was performed with SPSS/PC+, version 4.0.

RESULTS

Trapping pattern and age ratio

The following numbers of Little Terns were sampled: 513 birds in 1990, 629 in 1991, 601 in 1992, 536 in 1993, 677 in 1994. All birds were caught between periods 21 and 38 (Fig. 2); except for single birds on 12 May 1991, 20 May 1993, 24 September 1991, 25 September 1992. Large numbers of Little Terns joining the roost were recorded every year starting from period 28 (9-15 July). In period 26 (25 June-1 July) the first juveniles were caught. The proportion of juveniles in the population significantly increased from period 28 to period 36 (Fig. 2; Kendall rank correlation, \( \tau = 0.556, P = 0.037, n = 9 \)). Early in the season, a high proportion of juveniles still showed growing flight-feathers. Also the mean bill length of juveniles in periods 28 and 29 was significantly lower than in any other period, while no differences were observed among values of periods 32-36 (Table 1; one-way ANOVA, \( F_{5,536} = 21, P < 0.001 \), Student-Newman-Keuls test, \( P < 0.05 \)). Nevertheless, in periods 32-36 mean bill lengths of juveniles (26.3 mm) and adults (30.5 mm) still differed (\( t \)-test, \( t_{734} = -35.6, P < 0.001 \)). Percentages of juveniles in the central part of the season, from 23 July to 2 September (periods 30-35, selected in order to contain the two central quartiles of the distribution of this age class each year), were 12.2% in 1990, 20.3% in 1991, 32.1% in 1992, 24.9% in 1993, 34.8% in 1994, indicating significant differences (\( \chi^2 = 81.6, df = 4, P < 0.001 \)). Second-year birds were rather uncommon (maximum 24 individuals in 1993 and 1994, respectively 5.9% and 5.6% of the birds older than one year), although some might have been overlooked.

Origin of birds

We checked a total of 163 birds ringed else-
Table 1. Mean, standard deviation, range and sample size of bill length of juveniles (each period from 28 to 36) and adults (periods 32-36, grouped). Dates refer to the first day of each 7-day period.

<table>
<thead>
<tr>
<th>period date</th>
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<th>29</th>
<th>30</th>
<th>31</th>
<th>32</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>9 Jul</td>
<td>16 Jul</td>
<td>23 Jul</td>
<td>30 Jul</td>
<td>6 Aug</td>
</tr>
<tr>
<td>mean±SD</td>
<td>23.9 ± 1.1</td>
<td>23.1 ± 1.0</td>
<td>25.4 ± 1.9</td>
<td>25.3 ± 1.3</td>
<td>26.5 ± 1.5</td>
</tr>
<tr>
<td>range</td>
<td>22.2-26.0</td>
<td>21.3-24.9</td>
<td>20.8-28.3</td>
<td>21.4-28.3</td>
<td>23.7-30.7</td>
</tr>
<tr>
<td>n=</td>
<td>17</td>
<td>34</td>
<td>36</td>
<td>49</td>
<td>43</td>
</tr>
</tbody>
</table>

Table 2. Origin of Little Terns ringed as chicks and recovered in the same year at the study site. Numbers of ringed chicks refer to the period 1990-94.

<table>
<thead>
<tr>
<th>Colonies</th>
<th>distance (km)</th>
<th>direction (degrees)</th>
<th>ringed chicks</th>
<th>direct recoveries</th>
</tr>
</thead>
<tbody>
<tr>
<td>Southern Lagoon of Venice</td>
<td>20</td>
<td>220</td>
<td>262</td>
<td>12 (4.6%)</td>
</tr>
<tr>
<td>Po Delta</td>
<td>60</td>
<td>177</td>
<td>5865</td>
<td>133 (2.3%)</td>
</tr>
<tr>
<td>Lagoon of Grado and Marano</td>
<td>81</td>
<td>72</td>
<td>284</td>
<td>4 (1.4%)</td>
</tr>
<tr>
<td>Comacchio</td>
<td>93</td>
<td>191</td>
<td>803</td>
<td>7 (0.9%)</td>
</tr>
<tr>
<td>Inner Po river</td>
<td>93</td>
<td>234</td>
<td>117</td>
<td>4 (3.4%)</td>
</tr>
<tr>
<td>Cervia Saltpans</td>
<td>133</td>
<td>182</td>
<td>161</td>
<td>1 (0.6%)</td>
</tr>
<tr>
<td>Margherita di Savoia Saltpans</td>
<td>537</td>
<td>147</td>
<td>480</td>
<td>0 (0.0%)</td>
</tr>
</tbody>
</table>

where during the same calendar year (direct recaptures): only 2 of them had been ringed as full-grown, all the others as chicks in colonies up to 133 km away from the study area. One of the two birds ringed as full-grown originated from a spring migration stopover site along the coast of Tuscany, 254 km to the SW of the roost (S. Rossore, Fig. 1), whereas the other one had been ringed near a breeding colony in the Po Delta. The origin of birds ringed as chicks is shown in Table 2, the number of chicks ringed at each breeding area and the relative recovery rate at our study site being indicated. In total 23.3% of 691 first captured juveniles had been previously ringed as chicks. As regards birds ringed elsewhere in Italy in previous years, we caught 13 birds ringed as full-grown in years 1983-92 and 58 ringed as chicks in colonies up to 279 km away (Table 3) in years 1976-93 (oldest bird 18 years and 20 days, from Cervia, Fig. 1). Among birds ringed as full grown, 6 originated from a spring migration stopover site on the coast of Tuscany (Massaciucoli, Fig. 1), 6 had been ringed near the breeding colonies of the Po Delta and one at the nest in the southern part of the Lagoon of Venice. Two foreign recoveries were made: one bird ringed as chick in Norfolk, England, on 14 July 1986 and caught at our roost on 31 August 1993, another ringed as adult at the nest in Zeeland, the Netherlands, on 2 July 1991 was caught on 5 August.
Table 3. Origin of Little Terns recaptured in the study area and ringed as chicks in Italy in previous years.

<table>
<thead>
<tr>
<th>Colonies</th>
<th>distance (km)</th>
<th>recoveries</th>
<th>years elapsed from ringing</th>
</tr>
</thead>
<tbody>
<tr>
<td>Southern Lagoon of Venice</td>
<td>20</td>
<td>9</td>
<td>2, 3, 5, 6, 10</td>
</tr>
<tr>
<td>Po Delta</td>
<td>60</td>
<td>30</td>
<td>1, 2, 3</td>
</tr>
<tr>
<td>Lagoon of Grado and Marano</td>
<td>81</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Comacchio</td>
<td>93</td>
<td>9</td>
<td>1, 2, 3, 4, 9, 10, 11</td>
</tr>
<tr>
<td>Inner Po river</td>
<td>93</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>Cervia Saltpans</td>
<td>133</td>
<td>7</td>
<td>1, 2, 5, 9, 13, 18</td>
</tr>
<tr>
<td>Mezzana Bigli</td>
<td>279</td>
<td>1</td>
<td>13</td>
</tr>
</tbody>
</table>

Body mass

Mean body mass of juveniles was lower than that of adults in each period; this difference was significant (t-tests, \( P < 0.01 \)) in all periods but 29 and 36. Within each age class, mean body mass values showed highly significant differences among periods (Fig. 3; one-way ANOVA: \( F_{8,1920} = 64, P < 0.001 \) in adults; \( F_{8,654} = 23, P < 0.001 \) in juveniles). The coefficient of variation of body mass within each period increased by period 30 till period 35, both in adults and juveniles (Kendall rank correlation: \( \tau = 0.68, n = 7, P = 0.033 \) in juveniles; \( \tau = 0.88, n = 7, P = 0.006 \) in adults). The mean values of body mass of adults and juveniles showed an increase after period 32 (6-12 August): in adults each of periods 33-36 had a significantly higher value than any previous one, while among periods 28-32 only period 32 significantly differed from period 29; in juveniles there were no differences among periods 28-32, periods 33 and 34 had significantly higher values than periods 31 and 32, periods 35 and 36 had significantly higher values than any previous period (Student-Newman-Keuls test, \( P < 0.05 \)). Hence, both in adults and juveniles, period 32 divided the

Fig 3. Body mass of adult (A) and juvenile (B) Little Terns (mean, 95% confidence limits, range and sample size) in periods 28-36. Dates refer to the first day of each 7-day period.
minimum, median and maximum variation rates of body mass were +0.08, +0.2 and +0.6 g d⁻¹ in 9 adults and +0.09, +0.36 and +1.12 g d⁻¹ in 12 juveniles (difference between medians, Mann-Whitney test, n.s.). Body mass increased in some birds also before the end of period 32 (12 August), as it can be seen both from retraps (Fig. 4) and maximum recorded values of adults (Fig. 3A). Mean body mass of adults at departure, calculated on the upper quartile of the distribution for 84 birds in a suspended moult stage (RS= 0) was 63.6 g (n= 21). Assuming an initial mean

post-breeding season into two stages defined by different temporal patterns of mean body mass variation. The first one (periods 28-32) did not show any clear trend (linear regression: r= 0.03, \( F_{1,1034} = 0.76 \), n.s., in adults; r= 0.03, \( F_{1,237} = 0.18 \), n.s., in juveniles), while the second one (periods 32-36) had a highly significant increasing trend (linear regression: r= 0.40, \( F_{1,1069} = 203 \), \( P<0.001 \) in adults; r= 0.38, \( F_{1,484} = 83 \), \( P<0.001 \) in juveniles).

Individual birds trapped twice during the same season (considering only individuals ringed after the breeding season, i.e. 12 adults ringed after period 27 and 13 juveniles, all periods) also indicated a body mass increase (Fig. 4). Excluding one juvenile and three adults that lost weight, the

Fig. 4. Body mass variation of adult (A) and juvenile (B) Little Terns trapped twice during the same season (daily scale). Adults having more than a single growing primary when recaptured are indicated with solid dots.

Fig. 5. Primary moult of adult Little Terns in periods 21-37; (A) median, central quartiles and range of primary score, (B) median and range of the number of shed primaries (lines). Bars indicate percentages of birds with suspended moult (Raggedness Score, RS= 0) or birds which are going to suspend it (RS= 1). Dates refer to the first day of each 7-day period.
body mass of 48.2 g (all adults in periods 28-32, \(n=702\)) the average increase can be estimated at 15.4 g, which represents a 32% increase.

**Moult of primaries**

The earliest Little Terns replacing their primaries were observed on 12 June. By period 26 (25 June-1 July) more than 90% of the birds were in active wing moult. Fig. 5 shows the moult progress, expressed by moult score and by number of shed primaries; in Figure 5B the presence of birds which have reached the final condition of suspended moult can be seen too. Since the overall number of birds in a suspended moult condition was small (84), the moult stage at which suspension is achieved was determined adding to this sample 245 more birds with a single primary still growing and RS equal to 1, i.e. very likely to suspend the moult within very few days (Table 4). Moult never reached p9 and p10, the two outermost long primaries, being usually suspended at p6-p7 and rarely at p5 by the time the birds left the study area; only 6 birds going to suspend at p8 were recorded. A temporal variation in the point of suspension was found (Fig. 6), relative frequencies significantly differing among periods (\(\chi^2=38.97, df=10, P<0.001\); p5, p6, p7 were tested). Birds suspending later in the season showed a clear tendency to reach a slightly more advanced stage, with no difference in the temporal pattern of p5 (Kendall rank correlation, \(n=6, n.s.\)), a significant decrease of p6 (Kendall rank correlation, \(\tau=-1, n=6, P=0.005\)), a significant increase of p7 (Kendall rank correlation, \(\tau=0.73, n=6, P=0.039\)) and suspension at p8 being only observed after period 34 (20-26 August). Moult intensity, expressed by the number of simultaneously growing primaries, showed higher values in the early stages of this moult series, declining after p5 had been shed (Fig. 7).

**Table 4.** Number of adults with suspended primary moult (RS, Raggedness Score= 0) or going to suspend it (RS= 1) between primary 5 and 8.

<table>
<thead>
<tr>
<th>point of moult suspension</th>
<th>RS= 0</th>
<th>RS= 1</th>
<th>total</th>
<th>%</th>
</tr>
</thead>
<tbody>
<tr>
<td>p5</td>
<td>3</td>
<td>20</td>
<td>23</td>
<td>7.0</td>
</tr>
<tr>
<td>p6</td>
<td>59</td>
<td>115</td>
<td>174</td>
<td>52.9</td>
</tr>
<tr>
<td>p7</td>
<td>22</td>
<td>104</td>
<td>126</td>
<td>38.3</td>
</tr>
<tr>
<td>p8</td>
<td>0</td>
<td>6</td>
<td>6</td>
<td>1.8</td>
</tr>
<tr>
<td>total</td>
<td>84</td>
<td>245</td>
<td>329</td>
<td>100</td>
</tr>
</tbody>
</table>

Fig. 6. Points of moult suspension (p5-p8) in adult Little Terns in periods 32-37. Sample sizes on top. Dates refer to the first day of each 7-day period.

Fig. 7. Frequency of the number of simultaneously growing primaries related to the number of shed primaries in adult Little Terns. Sample sizes are shown above bars.
Three moulting birds retrapped 14 days after ringing showed a growth of p6 or p7 of 3 moult scores (from 1 to 4), i.e. more than two thirds of the feather length. Considering a mean external length of 89.9 mm (n= 17) for p6 and 101.4 mm (n= 20) for p7, a growth rate of 4.6-6.8 mm d^{-1} can be estimated. The median moult score difference for individual birds examined in two different years, each difference being corrected for temporal gap between ringing and retrap periods, was 2.82 (min= 0, max= 13.9, n= 40).

Some birds showing a second moult series were observed starting from period 29 (16-22 July). This series never reached p4 and only occurred in a small percentage of birds, up to 12.1% in period 32 (6-12 August). Birds with a suspended second series, moreover, might have been overlooked due to the very faint contrast between these new feathers and those just renewed in the previous series, which looked very fresh too.

**Moult and body mass variation**

The mean body mass of adults was almost constant until period 32 (6-12 August), when it started increasing (Fig. 3A); by that time, all birds had shed at least 3 primaries, the number of growing primaries decreased and the first cases of suspended moult were observed (Fig. 5B). The results of the multiple regression, performed to analyse the body mass variations in periods 32-36 with respect to the variables listed under Methods, showed that the variables entering in the equation, 7-day period and number of growing feathers (0 to 4), explained 28% of the body mass variance (r= 0.53, F_{2,717}= 142, P< 0.001). Therefore, a link between the onset of the pre-migratory body mass build-up and the last stages of moult is apparent. Moreover, in periods 32-36, body mass values of birds grouped according to the number of growing primaries significantly differed (Fig. 8; one-way ANOVA: F_{4939}= 64, P< 0.001); birds

**Table 5.** One-way ANOVA and Student-Newman-Keuls test (*= P< 0.05) among body mass values of adults grouped on raggedness score (RS) 0-4 in each period from 30-36 (cf. Fig. 9). Only birds with no or one growing primary were selected. Dates refer to the first day of each 7-day period.

<table>
<thead>
<tr>
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<th>n.s.</th>
<th>F_{4.105}= 5.2</th>
<th>P&lt;0.001</th>
<th>F_{4.139}= 9.6</th>
<th>P&lt;0.001</th>
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Fig. 8. Body mass of adult Little Terns with 0 to 4 growing primaries (mean, 95% confidence limits, range and sample size), captured between period 32 (6-12 August) and period 36 (3-9 September).
difference was suppressed by the increase of body mass of RS groups 2-3 starting from period 35, no significant differences between RS groups 1 to 4 being detectable in periods 35-36. In period 36 even the group RS= 0 did not significantly differ from any of the other groups (Table 5). Considering periods 33-36, a significant linear regression between body mass and 7-day period was observed in groups 0 to 3 (RS= 0, $r=0.26$, $F_{1,75}= 5.50$, $P= 0.022$; RS= 1, $r=0.28$, $F_{1,205}=17.7$, $P< 0.001$; RS= 2, $r=0.43$, $F_{1,149}=34$, $P< 0.001$; RS= 3, $r=0.38$, $F_{1,81}=13.9$, $P< 0.001$) but not in group 4 ($r=0.04$, $F_{1,29}=0.05$, n.s.), while in periods 30-33 regression was not significant in every group.

### DISCUSSION

#### Numbers, origins and phenology

The numbers of birds roosting at our study site are quite impressive in comparison with situations reported from other parts of the European range (up to 1200 birds together, Keijl & Koopman 1991; cf. also Glutz von Blotzheim & Bauer 1982). This fact is probably a direct consequence of the size of the breeding population over a catchment area which, as shown by many direct recoveries of juveniles ringed before fledging, was proven to extend at least up to 133 km away, covering all northern Adriatic coastal wetlands. The same origin can be supposed for adults as, in this species, juveniles are fed by parents for several weeks after fledging and many of them accompany parents on migration (Cramp 1985). The catchment area is probably larger than the northern Adriatic. Recoveries of chicks or breeding adults ringed in other years do actually include cases suggesting movements from inland areas of the Po Plain as well as some from north-western European colonies. Ringing results of 1995, not analyzed here, included the direct recovery of chick ringed in southern Italy, at Margherita di Savoia Saltlans, 537 km south-east of the roost.

Comparably large roosting flocks to that found in the Lagoon of Venice were never found elsewhere in Italy after the end of July, despite...
several surveys purposely carried out in August 1992-94 which revealed large flocks of other terns (*Sterna hirundo*, *S. sandvicensis*, *Chlidonias niger*) in all suitable areas along the western Adriatic coast till mid September (Casini *et al.* 1992; R. Rusticini, P. Utmar and M. Zenatello pers. comm.). Early in the season, the site was just occasionally used as an ‘off colony’ nocturnal roost, as described for the Least Tern (Atwood 1986), by a few pairs breeding in the vicinities. Some birds, probably those breeding within the Lagoon of Venice, seemed to rapidly move to the roost, as indicated also by the capture of a high proportion of juveniles not yet full-grown in periods 28-29, around mid-July. This behaviour was also described for the Least Tern, most juveniles (86.3%) leaving colonies within 3 weeks from fledging (Thompson & Slack 1984).

Before period 29 (16-22 July), the prevalence of unsuccessful breeders arriving from all northern Adriatic colonies could explain the low proportion of juveniles in our trapping samples. The progressively increasing proportion of juveniles since period 28 seemed, therefore, to be caused by breeders and offspring originating from the large colonies outside the Lagoon of Venice. Local breeding conditions and different distances between colonies and the roost would determine an asynchronous timing of the arrivals, ranging from period 28 (9-15 July) till period 32 (6-12 August), when peak numbers of Little Terns at the roost were recorded every year. The low number of local recaptures (both within-year and year-to-year), compared to figures of ringed birds, indicates that the size of the population yearly passing through the Lagoon of Venice ‘en route’ towards winter quarters is probably much higher than the number of Little Tern censused in any night between mid July and early September (5000-7000). In particular, spread timing of arrivals and low proportion of recaptures are indicative of a turnover in the population. Differences between years in the proportion of juveniles are most probably determined by the variability of breeding success at the largest colonies (cf. Burger 1984).

**Body mass and moult**

Both adults and juveniles show significantly increasing mean body masses only by the beginning of August (period 32), during a relatively short time before departing. Juveniles are always leaner than adults but show a similar pattern of body mass variation (Fig. 3). The wide range of arrival dates precludes a synchronous pattern of individual body mass increase. Some birds, in fact, reach a pre-migratory body mass already by period 32, when mean values have not shown any increase yet, while minimum values are relatively stable till period 35 (Fig. 3). Moreover, the coefficient of variation of body mass increases already by period 30 both in adults and juveniles, as a consequence of the contemporaneous presence of leaner individuals that have recently arrived and those already gaining body mass. Hence, also the body mass suggests the existence of a turnover, with most arrivals distributed between the beginning of July and early August (periods 28-32) and departures by early August (period 32) onwards. Moreover, the departure of some Little Terns well before the end of August is confirmed by a direct recovery: a juvenile ringed in period 30 (29 July 1992), which already by period 34 had moved 1100 km SW (caught 22 August 1992, Ebro Delta, Spain).

The timing of moult is about two weeks earlier at our study site compared to north-western Europe (Streichert 1982; Cramp 1985; Meininger *et al.* 1987). This probably results in a more advanced stage at which moult is suspended before the birds leave the breeding range (Fig. 5). These differences, in turn, may be determined by a 2-3 weeks anticipated breeding season in the Mediterranean Region (Cramp 1985), providing a longer period for wing moult before migration. Consistently with observations from other areas (Streichert 1982; Meininger *et al.* 1987), wing feather moult seems to prolong the stay of adults and to reduce their body mass increase rates (referred to the whole period of stay) as compared to juveniles. The year-to-year variation of individual moult schedules, falling in 80% of cases within a primary score of 5 (one feather), indicates that
single individuals maintain a similar moult timing in different seasons. The variability observed in our five year sample must, therefore, reflect also inter-individual differences unrelated to year (e.g. fixed individual strategies, location of breeding site, populations).

The post-breeding moult strategies adopted by many migrant species breeding at temperate latitudes often require a temporal segregation from other energy demanding processes (Payne 1972; King 1974; Hale 1980). In particular, in the case of strategies involving long non-stop flights, active moult and migration appear not to be compatible (Koopman 1986; Jehl 1987; Zwarts et al. 1990; Underhill et al. 1992; Piersma & Jukema 1993; Jenni & Winkler 1994). Nevertheless, a partial overlap between moult and breeding activity has been recorded in the Little Tern as well as in the Least Tern (Meininger et al. 1987; Thompson & Slack 1983). Similarly, in our case local retraps and the relation between mean values of body mass and number of growing primaries indicate that body mass build-up can also start before suspension, when the last moulted primary is still growing. The observed build-up, estimated at 15.4 g, is functional to a migratory strategy based on an initial step of 1074-1612 km (cf. Davidson 1984; flight speed 40-60 km h\(^{-1}\)). Premigratory body mass values are probably achieved only during the very last days before departure because of general disadvantages of bearing large reserve loads (decreased manoeuvrability and increased energetic cost of flight: Pennycuick 1975; Pienkowski et al. 1984; Lima 1986; Holmgren et al. 1993b), especially with a sub-optimal wing shape due to active moult. Individuals moulting early in the season keep feather growth and fattening separated, as low body masses of birds at last stages of moult in periods 30-33 indicate (Fig. 9). These birds, however, start gaining body mass shortly before the actual moult suspension, what results in higher body mass values of group with RS= 1 already by period 32. Birds starting the moult later could maintain the two processes separate only by anticipating the point of moult suspension to shorten the moult period, assuming that departure cannot be delayed beyond a certain date. This appears not to be the case, because the frequency of p5 as a point of suspension is not related with periods, lower points of primary moult suspension are never recorded and the most frequent point shifts from p6 to p7 (p8 being even reached). Hence, just the opposite tendency can be observed - part of the birds prolonging their stay in the moulting area and migrating with a more advanced stage of suspended moult. In order to cope with shorter time availability, birds approaching the last possible date for departure overlap feather growth with body mass build-up. While fattening at a RS= 1 does not seem to be forced by shortage of time, birds in less advanced stages of moult (RS 2-3) start to significantly overlap the two processes only by period 35 (27 August - 2 September), i.e. few days before all Little Terns leave the study area (Fig. 9). By this time, the positive correlations between body mass and 7-day periods for each group of RS= 0-3 might be explained by the progressive increase of the frequencies of birds that overlap the two processes and by the increase in the extent of overlap (Fig. 9). Shortage of time before departure from the moulting area, as a constraint for late moulters to overlap feather growth and body mass build-up, can also be deduced from the mass increase shown by the 'pre-suspended' moult category of Ruff Philomachus pugnax during the post-breeding season (Koopman 1986).

The time required for reaching pre-migratory body mass values is approximately the same as that required for growing two thirds of the length of p6 or p7 (10-14 days), assuming a daily mass increase (cf. Davidson 1984) of 2-3% of the lean mass (i.e. 1.0-1.5 g d\(^{-1}\) in Little Tern) and a feather growth rate of 4.6-6.8 mm d\(^{-1}\) (cf. Nadler 1978). Hence, if Little Terns had to migrate after moult suspension, there would be hardly any advantage to build-up energetic reserves still with RS greater than 3, i.e. when feather growth will continue for a longer time than the birds need to reach a pre-migratory body mass. The segregation of wing moult and body mass increase can be strongly adaptive, but a stronger inducement for
starting migration at an advanced point of moult suspension is revealed by Little Terns. Where local ecological factors allow the overlap between moult and body mass build-up, in case of shortness of time, the optimisation of the wing condition prevails over the segregation of the two processes. Such a hierarchy can be explained by feeding techniques of terns, largely dependent on flight ability, so that the best possible wing condition has to be maintained during the annual life cycle. The importance of the wing area also appears a reason why Little Terns adopt a moult strategy based on keeping a wing gap as small as possible, with a number of simultaneously growing feathers exceptionally exceeding 3, and the concurrent moult of different remex tracts (cf. Prevost 1983).

Moult migration
Post-breeding movements of Little Terns in the north-western Adriatic actually show many features of moult migration (Salomonsen 1968; Jehl 1990): the direction of these movements does not coincide with that expected for autumn migration, being actually opposite for the birds breeding south of the Lagoon of Venice; the high number of recoveries from the main breeding colonies and the absence of Little Terns in other Adriatic wetlands during August show that the Lagoon of Venice is probably the only moulting area in the north-western Adriatic wetland complex; the number of individuals is very high both with respect to the size of the Italian breeding population and to the size of roosts known from different countries. Differently from most Anatidae, Little Terns perform these movements regardless of age and sex, as a direct consequence of male and female sharing parental care and juveniles depending on parents for several weeks after fledging. In Shelduck *Tadorna tadorna*, Black-necked Grebe *Podiceps nigricollis* and Great-crested Grebe *Podiceps cristatus*, typical moult-migrants, both sexes also have a similar role during breeding and perform the moult migration with the same pattern; juvenile grebes are involved in such movements too (Salomonsen 1968; Storer & Jehl 1985; Piersma et al. 1986). The Lagoon of Venice can be considered distinct from the breeding areas as the distance from the nearest main colonies (Po Delta, 60 km to the south of the roost), is more than five times larger than the species’ home range during the breeding season (up to 10 km; Cramp 1985; Fasola & Bogliani 1990). Moreover, moult migration could also be suggested for other European populations of Little Terns, as large concentrations in July and August in Dutch Wadden Sea (Keijl & Koopman 1991) and post-breeding movements towards the Delta area, southwestern Netherlands (Meininger et al. 1987), might indicate.

The ultimate factor for developing moult migration by north-west Adriatic Little Terns is probably the different local food availability rather than the presence of places safe from predators. The birds do actually maintain flight capability during moult and their vulnerability to terrestrial predators in this season does not seem to be higher than in the rest of the year. Moreover, emergent sand banks similar to that in the study area are even more frequent in other Adriatic wetlands (Po Delta, Lagoon of Grado and Marano) than in the Lagoon of Venice and other tern species do in fact roost there throughout the month of August. Critical ecological factors which would determine the importance of the Lagoon of Venice for Little Terns in the period between breeding and departure to winter quarters, have yet to be discovered.

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**Samanvattning**

die nog laat ruien (na 27 augustus) kunnen tegelijkertijd in gewicht toenemen. Dit toont aan dat rui en 'opvetting' op hetzelfde tijdstip kunnen plaatsvinden. De trek van Dwergsterns naar de lagune van Venetië, na de broedtijd maar voor het uiteindelijke vertrek naar de wintergebieden, voldoet aan de gangbare definitie van ruitrek. (JvdM)

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