INTRODUCTION

Growth rates of chicks are important because growth may influence future survival and reproduction (Bolton, 1991). Chick growth can be affected both by prehatch (i.e. egg size) and posthatch (i.e. parental care) factors (Risch and Rohwer, 2000). The main prehatch factor affecting egg size is food availability (see e.g. Hébert and Barclay, 1988; Hiom et al., 1991; Bolton et al., 1992; Pons and Migot, 1995), so egg size reflects the conditions of food availability in the area surrounding colonies.
during the period of egg formation (Bolton et al., 1993). The main posthatch factor is parental quality through the amount and quality of food delivered to chicks (see e.g. Nisbet, 1978; Coulson and Porter, 1985; Bolton, 1991; Risch and Rohwer, 2000).

We performed an experiment to separate the effects of prehatch and posthatch factors on the growth rates of the chicks of Audouin’s Gull Larus audouinii. Nestlings hatched from large eggs were reared under food-stress conditions by wild parents (i.e. during the 1993 trawling moratorium that coincided with the chick-rearing stage in the Ebro Delta preventing chicks to be fed with fishing discards at a usual rate) (Oro et al., 1996b). Chicks hatched from smaller eggs from the Columbretes Islands were reared during the 2000 breeding season under ad libitum feeding conditions (captivity).

**METHODS**

Eggs were laid under periods of normal food availability (i.e. May) both at Columbretes Islands and the Ebro Delta, since the trawling-fishing moratorium was not implemented until June-July (Oro et al., 1996a; Columbretes wardens, pers. comm.). Ninety-seven eggs from Columbretes and 217 eggs from the Ebro Delta were measured with a digital caliper to the nearest 0.05 mm to obtain the volume. Egg volume was estimated from the equation (Hoyt, 1979),

\[ \text{Egg volume (cm}^3) = 0.000467 \times \text{length (mm)} \times \text{width}^2 \](mm)

Egg measurements were done by two different teams but following the same procedure (D. Oro at the Ebro Delta and EV and BS at the Columbretes Islands). Egg measurements do not necessarily correspond to the eggs from which our chick measurements were taken. However, we assume that egg measurements from the Ebro Delta and Columbretes Islands were representative of both colonies since sample sizes were large.

At the Ebro Delta nests were surrounded by a wire fence (see Oro et al., 1996a) and 106 chicks were measured (wing length and weight) every three days from hatching to fledging. Wing length was measured by means of a digital caliper to the nearest 0.05 mm and weight by means of several spring balances (50 ± 1 g, 100 ± 5 g, 500 ± 10 g).

Forty-five chicks from the Columbretes Islands were taken into captivity and fed ad libitum with fish at the facilities of the Centro de Protección y Estudio del Medio Natural of the Valencian Government. Each chick was measured (wing length and weight) every three days from hatching to release. Wing length was measured with a ruler to the nearest 0.5 mm and weight by means of a digital balance to the nearest 0.05 g.

Chick measurements from the Ebro Delta and Columbretes were also done by the same two teams. Only those variables measured following the same field procedures were considered in this study (i.e. weight and wing length).

Data analysis was carried out by means of an SPSS package (SPSS for Windows, Re. 10.0.6., 1999). For the analysis of the average weight gain curve, the straight (age classes 2 to 9) and the

**Table 1.** Mean weight and wing length for captive and wild-reared Audouin’s gull (Larus audouinii) chicks for each age class. Each age class includes periods of three days. SE = Standard Error.

<table>
<thead>
<tr>
<th>Age class</th>
<th>Captivity Weight (g)</th>
<th>Wild Weight (g)</th>
<th>Captivity Wing length (cm)</th>
<th>Wild Wing length (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>42.82 0.61 49.23 0.43</td>
<td>2.74 0.03 2.32 0.02</td>
<td>2.74 0.03 2.32 0.02</td>
<td>2.74 0.03 2.32 0.02</td>
</tr>
<tr>
<td>2</td>
<td>72.61 1.91 96.32 2.48</td>
<td>3.63 0.06 3.22 0.05</td>
<td>3.63 0.06 3.22 0.05</td>
<td>3.63 0.06 3.22 0.05</td>
</tr>
<tr>
<td>3</td>
<td>132.50 3.72 134.21 4.16</td>
<td>5.12 0.12 3.82 0.10</td>
<td>5.12 0.12 3.82 0.10</td>
<td>5.12 0.12 3.82 0.10</td>
</tr>
<tr>
<td>4</td>
<td>218.64 5.93 193.09 7.86</td>
<td>7.51 0.17 6.01 0.28</td>
<td>7.51 0.17 6.01 0.28</td>
<td>7.51 0.17 6.01 0.28</td>
</tr>
<tr>
<td>5</td>
<td>291.00 7.26 242.11 15.76</td>
<td>10.98 0.27 7.85 0.44</td>
<td>10.98 0.27 7.85 0.44</td>
<td>10.98 0.27 7.85 0.44</td>
</tr>
<tr>
<td>6</td>
<td>384.39 8.00 331.69 14.85</td>
<td>15.38 0.33 12.94 0.44</td>
<td>15.38 0.33 12.94 0.44</td>
<td>15.38 0.33 12.94 0.44</td>
</tr>
<tr>
<td>7</td>
<td>446.39 8.46 434.23 21.99</td>
<td>18.85 0.41 17.15 0.74</td>
<td>18.85 0.41 17.15 0.74</td>
<td>18.85 0.41 17.15 0.74</td>
</tr>
<tr>
<td>8</td>
<td>501.20 7.70 476.31 16.64</td>
<td>22.36 0.34 20.75 0.74</td>
<td>22.36 0.34 20.75 0.74</td>
<td>22.36 0.34 20.75 0.74</td>
</tr>
<tr>
<td>9</td>
<td>539.96 9.28 494.23 15.25</td>
<td>24.91 0.41 24.37 0.51</td>
<td>24.91 0.41 24.37 0.51</td>
<td>24.91 0.41 24.37 0.51</td>
</tr>
<tr>
<td>10</td>
<td>577.81 11.55 475.71 22.48</td>
<td>28.17 0.48 26.07 0.78</td>
<td>28.17 0.48 26.07 0.78</td>
<td>28.17 0.48 26.07 0.78</td>
</tr>
<tr>
<td>11</td>
<td>592.52 12.09 505.00 23.45</td>
<td>30.68 0.24 28.78 0.60</td>
<td>30.68 0.24 28.78 0.60</td>
<td>30.68 0.24 28.78 0.60</td>
</tr>
<tr>
<td>12</td>
<td>586.42 10.99 - -</td>
<td>32.78 0.33 - -</td>
<td>32.78 0.33 - -</td>
<td>32.78 0.33 - -</td>
</tr>
<tr>
<td>13</td>
<td>584.30 12.04 - -</td>
<td>34.71 0.23 - -</td>
<td>34.71 0.23 - -</td>
<td>34.71 0.23 - -</td>
</tr>
<tr>
<td>14</td>
<td>578.37 11.27 - -</td>
<td>35.78 0.34 - -</td>
<td>35.78 0.34 - -</td>
<td>35.78 0.34 - -</td>
</tr>
<tr>
<td>15</td>
<td>572.75 14.13 - -</td>
<td>37.23 0.27 - -</td>
<td>37.23 0.27 - -</td>
<td>37.23 0.27 - -</td>
</tr>
<tr>
<td>16</td>
<td>556.67 25.98 - -</td>
<td>36.77 0.96 - -</td>
<td>36.77 0.96 - -</td>
<td>36.77 0.96 - -</td>
</tr>
</tbody>
</table>
asymptotic (age classes 10 to 16) phases were considered separately. Mean growth rates in the linear stage (i.e. slopes), asymptotic means from both locations and mean egg volume were compared by means of t-tests (two-tailed) and Mann-Whitney U-tests (Zar, 1999).

RESULTS

Average weight gain for each 3-day age class of Audouin’s Gull chicks from the Ebro Delta and captivity are shown in Table 1 and Figure 1. Captive-reared chicks (age class 1) hatched with a lower mean weight than wild ones (U = 690.5, P = 0.0001). Weight gain rates from age classes 2 to 8 were not significantly different (t = 0.53, P = 0.609) but the asymptotic weight of the captive-reared chicks was significantly higher than that of wild ones (t = 4.07, P < 0.001).

The average increase in wing length for each age class of Audouin’s Gull chicks from the Ebro Delta and captivity is displayed in Figure 2. Captive-reared chicks hatched (age class 1) with a higher mean wing length than wild ones (U = 234.5, P = 0.0001). However, wing length growth rates from age classes 2 to 8 were not significantly different (t = 0.35, P = 0.735) between captive and wild-reared chicks. Since wing measurement data from the asymptotic region for wild chicks were missing, we were not able to compare them with captive-reared chicks.

The mean volume of eggs from the Columbretes Islands and the Ebro Delta are shown in Figure 3. Eggs from the Ebro Delta were significantly larger than those from the Columbretes Islands (U = 7768.0, P = 0.0002).

DISCUSSION

The fact that eggs from the Ebro Delta were larger than eggs from Columbretes suggests a better mean body condition of the Ebro Delta females. Though eggs from the Columbretes Islands were smaller and chicks hatched with a lower mean weight than chicks from the Ebro Delta, the asymptotic weight of chicks from Columbretes eggs was finally higher. This suggests that posthatch factors (i.e. amount of food delivered especially during the last phases of chick growth) have a stronger influence on the final chick mass than prehatch factors (i.e. egg size), as previously indicated by Bolton (1991). According to sex ratio theory (Oddie, 1998; Nager et al., 1999) females under food-stress conditions would favor the production of female offspring. This could explain why chicks from the Ebro Delta had a lower asymptotic weight if reproductive females from the Ebro Delta were shown to be food stressed and assuming that female chicks weigh less...
on average than male chicks. However, the food-stress period in the Ebro Delta did not coincide with the pre-incubation period (i.e. when sex would be determined in the egg) but with the chick-rearing period. Hence, the differences observed cannot be explained by skewed sex ratios.

The fact that captive-reared chicks reached their fledging period with a higher mass than chicks from wild gulls but had similar growth rates during the early phase of growth suggests that wild gulls were not able to provide as much food as chicks can eat. This could be due to the conditions of reduced food availability at the Ebro Delta caused by the trawling-fishing moratorium. Alternatively, wild gulls from the Ebro Delta could be subjected to a trade-off between present and future reproduction, as predicted by life-history theory (Reznick, 1985). Fledging size seems to be determined during the beginning of the asymptotic phase, both for wing length and weight, the phase of linear growth not being very relevant. Finally, egg size did not have any influence on the wing length of hatchlings. This is probably related to the fact that wing length at hatching time is less important for survival than at fledging time (Soler and Soler, 1990).

The future demographic consequences (e.g. influence on survival, recruitment and life-time reproductive performance) of reduced food availability for chicks from the 1993 Ebro Delta cohort should be explored in further work.

ACKNOWLEDGEMENTS

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