BREEDING BIOLOGY OF A KENTISH PLOVER (CHARADRIUS ALEXANDRINUS) POPULATION IN AN INLAND SALINE LAKE

Rosendo M. FRAGA* and Juan A. AMAT**

SUMMARY.—Breeding biology of a Kentish Plover (Charadrius alexandrinus) population in an inland saline lake. We studied the breeding biology of Kentish Plovers (Charadrius alexandrinus) in Fuente de Piedra lake (southern Spain) in 1991 and 1992. Breeders showed sexual dimorphism in tarsal length and body mass; body mass decreased throughout the breeding season only in males. Laying dates spanned 88 days in 1991 and 110 in 1992. Eggs deposited in the late nesting season were larger than those in the beginning of the season. Females incubated during daytime and males during the night. Apparent clutches of 1-2 eggs occurred mostly late in the nesting season and reflect a high incidence of partial predation (recorded in 17% of 288 2-3 egg clutches). Nest predation increased in the course of the breeding season, and only 19% of all clutches produced chicks. Variables measured for each nest site (nest cover, distances to water and to nearest neighbour) did not influence nest predation. Kentish Plover pairs that lost clutches usually renested together, on average 11-24 days after loss of their previous clutch. The body masses of females were similar between first and subsequent replacement nestings. Biparental care of chicks lasted longer than in several other populations of Kentish Plovers. When the chicks were 15-20 days old one of the adults, usually the female, deserted the brood. Gull-billed Terns (Gelochelidon nilotica) preyed on chicks up to 16 days of age. Both sexes showed antipredator behaviours (alarm calls, mobbing). Possibly, the greater maternal protection of the brood at Fuente de Piedra compared to other breeding locations results from an interrelationship between high predation pressure and type of predators, since mobbing of Gull-billed Terns by adult plovers was effective in deterring the terns. After deserting broods, some females mated to new males (sequential polyandry). Sequential polygyny was recorded in males that fledged chicks early enough for a subsequent nesting attempt. We propose that the duration of the breeding season and high clutch failure rates constrained the frequency of sequential polygamy in our population.

Key words: breeding biology, brood desertion, Charadrius alexandrinus, parental care, mating system, sequential polygamy.

RESUMEN.—Biología de la reproducción de una población de Chorlitejos Patinegros (Charadrius alexandrinus) en una laguna salada interior. Este estudio documenta diversos aspectos de la biología de la reproducción de los Chorlitejos Patinegros (Charadrius alexandrinus) en la laguna de Fuente de Piedra (sur de España) en 1991 y 1992. Los individuos nidificantes mostraron dimorfismo sexual en longitud del tarso y masa corporal; la masa corporal de los machos disminuyó a lo largo del período reproductor. Las fechas de puesta abarcaron 88 días en 1991 y 110 en 1992. Los huevos depositados al final de la estación reproductora fueron mayores que los del comienzo. Las hembras incubaron de día y los machos de noche. Las puestas de 1-2 huevos se observaron principalmente al final de la estación de nidificación y podrían ser el resultado de la predación parcial (registrada en el 17% de 288 puestas de 2-3 huevos). Hubo un incremento en la predación de nidos al ir avanzando la estación de reproducción y sólo el 19% de las puestas produjo pollos. Las características de los sitios de nidificación (cobertura de los nidos, distancias al agua y al vecino más próximo) no influyeron en el éxito de los nidos. Las parejas de chorlitejos que perdieron las puestas tendieron a renidificar juntas, por término medio 11-24 días tras la pérdida de las puestas precedentes. Las masas corporales de las hembras fueron similares entre las primeras y las siguientes nidificaciones de reemplazamiento. El cuidado biparental de los pollos duró más que en otras localidades. Cuando los pollos tuvieron 15-20 días uno de los adultos, generalmente la hembra, abandonó la nidada. Las Pagazas Piconegrandas (Gelochelidon nilotica) preñaron sobre pollos de chorlitejo de hasta 16 días de edad. Ambos sexos mostraron comportamientos anti-predador. Posiblemente, la mayor duración del cuidado maternal de las nidadas en Fuente de Piedra que en otras localidades se debe a una...
interrelación entre las altas tasas de predación y el tipo de predadores, ya que los ataques de los chorlitejos adultos sobre las pagazas resultaron efectivos, al conseguir alejar a los predadores de los sitios donde se hallaban los pollos. Tras desertar de las nidadas, las hembras se emparejaron con otros machos, probándose así la polianidria secuencial. Una vez que los pollos volaron, se registró poliginia secuencial en machos que dispusieron de tiempo suficiente para un nuevo intento de nidificación. Proponemos que la duración de la estación de reproducción y los niveles de fracaso de nidos limitarían la frecuencia de poligamia secuencial.

Palabras clave: biología de reproducción, cuidado parental, Charadrius alexandrinus, deserción de la nidada, poligamia secuencial, sistema de emparejamiento.

INTRODUCTION

Kentish Plovers (Charadrius alexandrinus) probably offer one of the best systems for the study on avian mating systems and parental care. The species breeds in four continents, and the occupied habitats include seacoasts, salt flats, grazed grasslands and inland lakes. A variety of breeding systems has been described in Kentish Plovers from southern France, California and Hungary (Lessells, 1984; Warriner et al., 1986; Székely & Lessells, 1993). On the one hand, in some populations the females desert their first brood when the chicks are 6-15 days old and mate with a new male (sequential polyandry), and several cases of sequential polygyny have also been observed in males (Warriner et al., 1986). On the other hand, other studies report almost exclusive monogamous pair bonds in Germany (Rittinghaus, 1956). These observations suggest that the mating behaviour of individuals may be different in some populations, and that the population strategies may be different in different geographic locations. The opportunities for mate change should increase with the length of the nesting season, and should also be higher in areas where the chances of rearing a first brood are higher, such as the areas with reduced predation on eggs and chicks (Warriner et al., 1986). However, the estimation of remating frequencies is difficult, because plovers may move for long distances between changes of mates (Székely & Lessells, 1993; Stenzel et al., 1994; Jonsson, 1995).

The breeding biology and parental behaviour of Kentish Plovers have been studied at several coastal sites in Europe (Rittinghaus, 1975; Lessells, 1984), California (Warriner et al., 1986), Egypt (Simmons, 1951) and Japan (Nakazawa, 1979), as well as at some inland localities, both in Europe (Székely, 1992; Székely et al., 1994; Székely & Williams, 1994) and North America (Purdue, 1976a, 1976b; Page et al., 1983; Warriner et al., 1986; Paton & Edwards, 1990; Paton 1995). However, no large scale study of Kentish Plovers has been carried out in Spain (but see Sánchez et al., 1990; Ballesteros & Torre, 1993; Torre & Ballesteros, 1994; Figuerola & Cerdá, 1995), although this country harbours some of the largest European populations (Tucker & Heath, 1994). In this paper we report on the breeding biology and parental care of Kentish Plovers from a large saline lake in Spain. We provide this information in the context of mate desertion. Thus, we aimed to investigate why and when should a parent desert its brood and possibly remate.

MATERIAL AND METHODS

The study was carried out in 1991 and 1992 at the Laguna de Fuente de Piedra, Málaga Province, S. Spain (37°06' N, 4°45' W, altitude 410 m a. s. l.), which is a shallow (<60 cm deep) saline lake covering 1300 ha. The lake is a nature reserve and has been described elsewhere (Vargas Yáfiez et al., 1983; García & Niell, 1993). The climate is dry Mediterranean, with an average yearly rainfall of 466 mm (n = 29 years). Most rain falls in winter (September to April), but irregular summer storms may occur. The lake is endorheic and seasonal, and although it dries up in summer the soil remains wet throughout most of the summer. In the lake there are some dykes and islets that were constructed during the last century when the salt was commercially exploited.

Although 1991 was less rainy than 1992, water levels were higher during the former...
year because the winter 1989/90 was very rainy, and the lake remained flooded throughout 1990 throughout July 1991. The natural vegetation consists of halophytic shrubs (mostly *Arthrocnemum glaucum* and *Suaeda vera*) with some *Tamarix africana* trees and beds of *Phragmites communis* in a channel that surrounds the lake. The unusual high water levels during 1990 determined the death of many shore plants, particularly *A. glaucum*.

To estimate the size of the population breeding at Fuente de Piedra, we conducted censuses throughout the breeding seasons using binoculars and a telescope. These counts were made in the morning and we only recorded those individuals that were out of nests, i.e. non-incubating birds.

Data taken from nests included cover and distances to water and to the nearest active conspecific nest. Nests were allocated to cover categories defined as follows: 0 when the nest was completely exposed, and 1-3 when the nest was visible from >75%, 75-25%, and <25%, respectively, from about 1.5 m above the nest. To see if the nest cover categories provided a reliable estimate of nest visibility, and hence potential vulnerability to visually searching nest predators, once the nesting season of 1991 had finished, and during two consecutive days between 10:00 and 14:00 h, we measured solar irradiance on the horizontal plane at the center of each nest scrape and also at a completely exposed site 1 m from the nest site, by using a LI-COR pyranometer sensor LI-200SZ. Solar irradiance at each nesting site was expressed as the percentage of that recorded at the site relative to that recorded at the corresponding exposed site. Differences in solar irradiance among nest cover categories were then assessed with an ANOVA on arcsin-transformed data. The result was significant ($F = 38.85$, $P < 0.001$), indicating that the cover categories we used related to the amount of solar radiation each nest received from above. Distances from nest to water were estimated by eye at the moment of nest discovery. Distances to the nearest neighbour nest were measured with a tape if <100 m, by walking if they were 100-300 m, and on an aerial photograph if >300 m.

Egg length and width were measured with a vernier caliper to the nearest 0.1 mm, and eggs were weighed every 3-6 days with a portable Sartorius balance (accuracy 0.1 g). Egg volumes were estimated with the formula of Douglas (1990): $V_e = K_v L^2 W^2$, where $K_v = 0.5236 - (0.5236 \times 2(L/W)/100)$, $L =$ egg length (cm) and $W =$ egg width (cm). The relationship between mass of fresh eggs ($MFE$) and $V_e$ was described by the regression equation $MFE = 0.604 + 0.935 V_e$ ($r^2 = 0.92$, $n = 88$ eggs (each egg from a different clutch), $P < 0.001$). Eggs lost on average 0.0474 g per day during incubation. For clutches found during incubation we estimated the date of egg laying by the equation: $Days_{since}laying = (MFE - OM)/0.0474$, where $OM =$ observed mass. We took the mean estimated date of eggs for the clutch. We checked the accuracy of these estimates on 15 eggs (one from each clutch) of 1993 for which we knew their egg-laying dates. On average, laying dates were underestimated by $2.38 \pm 1.88$ days. Nest contents were checked every 1-2 days during the laying period, and every 3-6 days during incubation, until their fates were known.

We captured adult plovers in the nests with funnel traps. We captured plover chicks at hatching time in the nest, or later with a hand net. All individuals were marked with numbered aluminium rings (from the Spanish National Parks Service, ICONA) and four coloured rings in unique combinations. We took biometry data (mass, tarsus length, culmen length) from adults and chicks, and also wing length in adults. Culmen and tarsus lengths were measured to the nearest 0.1 mm using a vernier caliper, wing length was measured with a rule to the nearest mm, body masses of adults were recorded with a spring Pesola balance to the nearest g, and body masses of chicks were recorded with a portable Sartorius balance to the nearest 0.1 g. The three morphological variables measured in chicks were all correlated with chick age (for chicks with known hatching date). To estimate the age of chicks with unknown hatching dates we used the equation of Székely & Lessells (1993): $Age (in d ) = 16.05 - (ln(40 - body mass (in g))/body mass)/0.117$.

Data on parental care and on the attendance of broods were obtained either from focal observations of ringed families (each
Sexual dimorphism in body mass, and culmen, wing and tarsal lengths (means ± SD) among breeding Kentish Plovers. Masses are in g, lengths in mm.

[Dimorfismo sexual en masa corporal y longitudes de culmen, ala y tarso (valores medios ± desviación típica) de Chorlitejos Patinegros durante el período de nidificación. Las masas corporales se expresan en g, las longitudes en mm.]

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<td>Males (n = 154)</td>
<td>43.1 ± 2.8</td>
<td>15.1 ± 0.8</td>
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<td>Females (n = 158)</td>
<td>42.2 ± 3.0</td>
<td>15.1 ± 0.7</td>
<td>111.0 ± 3.3</td>
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<td>r-test</td>
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lasting up to 3 h) carried out from a portable hide or a parked car, or by one of us watching the adult plovers while their chicks were pursued, captured and handled (a process usually taking more than 5 min). The latter method was used by Lessells (1984) to assess the timing of brood desertion, because the off-duty parent, if present in the area, usually returns to the brood when the duty parent begins to perform alarm calls.

We also regularly visited four smaller lakes within 15 km of Fuente de Piedra (Gosque, Ratosa, Salada de Campillos, Capacete) searching for Kentish Plovers ringed in Fuente de Piedra. We recorded there some colour ringed individuals, but no nests of birds ringed in Fuente de Piedra nor marked adults with chicks were observed in these lakes.

Throughout the paper, mean values are reported ± 1 s.d.

RESULTS

The local plover population

Through repeated censuses during the breeding season we estimated that 200-300 plovers nested in Fuente de Piedra. Kentish Plovers occurred at Fuente de Piedra every month, although in late August and September, when the lake surface was almost completely dry, they were present in lower numbers. Individuals ringed at Fuente de Piedra were sighted in some nearby lakes. Some marked individuals were seen in Cádiz Bay (145 km to the WSW), the mouth of the Guadalhorce River near Málaga (55 km to the S), Laguna del Gobierno (Sevilla province, 50 km to the NW) and Salinas de Guardias Viejas (Almería province, 195 km to the ESE). Most of these observations were reported during the period when fewer Kentish Plovers were found at Fuente de Piedra. We have no further information on movements despite our repeated search for marked Kentish Plovers in Cádiz Bay, the main locality for the species in southern Spain.

An indication of philopatry was the finding of nests of individuals ringed as chicks in the lake by M. Rendón 3-5 years before our study (three females and one male, out of 17 birds). In addition, 8.3% of the chicks (N=84) that we ringed in 1991, bred in Fuente de Piedra in 1992. Site-fidelity was suggested by our own ringing data, as individuals of both sexes captured in nests in 1991 were re-trapped in nests in 1992. Return rates based on such recaptures were 40.3 % (23/57) for females, and 54.9 % (28/51) for males. We suggest that both figures are underestimates, because many nests in 1992 escaped detection or were predated before the adults could have been caught.

There were significant sexual differences in tarsus length and body mass (Table 1), with males being slightly but significantly larger. No sexual differences were found in culmen and wing lengths (Table 1). Body masses of males and females did not show significant differences between the breeding seasons of 1991 and 1992. We found significant monthly
changes in the body mass of male plovers (one-way ANOVA: $F=2.84$, $P=0.025$), with the highest mass in March-April, and a minimum in May and June (Fig. 1). No similar trend was detected in breeding females ($F=0.28$, $P=0.893$, Fig. 1).

### Breeding ecology

**a) Laying dates**

The egg-laying season in 1991 lasted from 29 March to 25 June (88 days) (median: 22 May) and in 1992 from 11 March to 29 June (110 days) (median: 11 May, Fig. 2). In both years we visited the study area from late February to mid-August, so the difference between years seems real.

**b) Nest sites**

The nests were shallow scrapes, sometimes partially filled with pebbles, small snail shells, pieces of dry mud or vegetation. Some females deposited eggs in scrapes containing eggs of another female (see below). Other females deposited clutches in scrapes of successful or depredated nests within 2 days of hatching or predation. Reutilization of nest scrapes within the nesting season involved 6.0% of 316 nesting attempts. In 1992, a nest scrape was used four times (three times by the same pair), and another one was used three times.

Nest cover was 0 for 48.8% of 316 nests. Nest cover categories 1 to 3 comprised 22.7%, 16.8%, and 11.8%, respectively. Nests placed under vegetation were located either under dead plants or green plants. The plant species used more commonly for nesting was Arthrocnemum glaucum. Nest cover showed no significant changes between years ($\chi^2=4.57$, $P=0.206$) or months ($\chi^2=6.68$, $P=0.661$).

The other two variables describing nest location are summarized in Fig. 3. Median distance to water was 7 m in 1991 ($n=79$) vs. 20 m in 1992 ($n=157$) (Mann-Whitney U-test, $U=4199.5$, $P<0.001$), probably reflecting the higher water levels of the lake during the first year. Nest spacing was similar in both years, with median distances to the nearest neighbour of 29 and 32 m in 1991.
c) Clutch sizes

If clutch size is defined as the maximum number of eggs observed in a nest, we found 232 of 316 nests (73.4%) containing three eggs, and 52 and 32 nests with two and one egg, respectively. Except in a few cases (see below), one-egg clutches were not incubated. The mean clutch size was 2.63 eggs, and the median and mode three eggs. In addition, 3 nests had five or six-egg clutches. The different colouration and size, as well as the laying sequence (in two nests), indicated that clutches of more than three eggs were produced by two females.

Due to the high rate of predation on eggs (see below), many clutches of less than three eggs could have suffered partial predation before we found them. Clutch sizes significantly differed between years ($\chi^2 = 8.657$, df = 2, $P = 0.013$). Moreover, the differences in clutch size between months were significant (Table 2; $\chi^2 = 32.28$, df = 6, $P < 0.001$) and exhibited similar trends in 1991 ($\chi^2 = 9.88$, $P = 0.04$) and 1992 ($\chi^2 = 27.91$, $P < 0.001$). Three-egg clutches were more common at the beginning.
Table 2

Frequencies of clutch sizes of Kentish Plovers over the breeding season (number of nests).

[Cambios mensuales en el tamaño de puesta (número de nidos) de los Chorlitojos patinegros.]

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<td>3</td>
<td>34</td>
<td>62</td>
<td>80</td>
<td>58</td>
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<tr>
<td>Mean clutch</td>
<td>2.86</td>
<td>2.76</td>
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of the season (in 91.9% of the March nests) and declined towards summer (54.7% of June nests). This steep decline in clutch size could reflect increased partial predation, and perhaps laying patterns as well (see below). Females incubating two-egg clutches did not differ in body mass from those incubating three eggs ($t = 0.30, P = 0.762$).

d) Egg dimensions and masses

Mean dimensions of 751 eggs were $31.99 \pm 0.11$ mm (length) and $23.43 \pm 0.06$ mm (width). Mean egg volume was $8.96 \pm 0.65$ cm$^3$. Egg volumes, calculated as average for each clutch, were larger in 1992 than in 1991 ($9.03 \pm 0.59$ vs. $8.81 \pm 0.62$ cm$^3$, $t = 2.86$, $P = 0.005$, $n = 228$ and $n = 88$ clutches, respectively). Average egg volume for each clutch also showed significant monthly changes (one-way ANOVA, both years combined, $F = 2.66$, $P = 0.048$), with a tendency to increase throughout the season (March: $8.82 \pm 0.62$ cm$^3$, $n = 39$ clutches; April: $8.89 \pm 0.66$, $n = 71$; May: $8.94 \pm 0.58$, $n = 97$; June: $9.10 \pm 0.58$, $n = 96$). Mean clutch volume was $26.85 \pm 1.82$ cm$^3$ ($n = 228$ three-egg clutches). Clutch volume (three-egg clutches) increased with female mass ($r = 0.34$, $n = 199$, $P < 0.001$, both years combined) and laying date in 1992 ($r = 0.25$, $n = 156$, $P = 0.002$), but not in 1991.

e) Nest attendance

Fig. 4 shows the hours of capture for both sexes throughout the incubation period. Both parents were caught together on 12 occasions. The relationship between incubating sex and time of day was evaluated using logistic regression with binary response (male or female incubating). The sex of the incubating parent was strongly related to time of day, with females incubating during daytime and males during the night (Fig. 5; Wald $\chi^2 = 65.53$, $P < 0.001$). However, there were some seasonal differences in incubation patterns. When ambient temperatures were high (>30°C, from late May onwards) males also tended to spend some time during the day at nests, mainly around midday (J. A. Amat unpubl.). Although our study was not specifically designed to investigate nest attendance, these trapping patterns likely reflect incubation schedules. Casual observations of nests of ringed pairs showed a concordant schedule of nest attendance.

Nest fates

The major outcomes for the Kentish Plover nests ($n = 316$) were desertion (14.2%), predation (62.6%), or the hatching of at least one chick (19.3%). Other nests (3.8%) failed to hatch from other causes, like flooding after rainstorms, or had unknown outcomes. Nesting success was higher in 1991 (29.2%) than in 1992 (15.6%) (Table 3; $\chi^2 = 7.79$, $P = 0.02$). In 1991 the three major categories of nest fate did not show monthly changes $\chi^2 = 3.72$, $P = 0.446$, but this was not so in 1992 (Table 4; $\chi^2 = 16.92$, $P = 0.009$), when there was
a decline in nesting success from March (29.7%, a level comparable to that of 1991), to the end of the nesting season. Such a trend was due to a seasonal increase in predation levels (Tables 3 and 4), and roughly parallels the data on apparent clutch size discussed before (Table 2).

Nest fate was unrelated to the degree of nest cover ($\chi^2 = 5.20$, $P = 0.519$). Likewise, we found no effect of distance to water on nest success (Kruskal-Wallis analysis of variance, $H = 3.19$, $P = 0.203$), or of the distance to the nearest nest on success ($H = 1.03$, $P = 0.598$).

**Table 3**

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<td>June</td>
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a) Nest desertion.

Clutches which were no longer incubated were regarded as deserted. All but two clutches of one egg, as well as the three nests containing 5 or 6 eggs, were apparently not incubated. No variable other than clutch size was clearly associated with nest desertion.

![Fig. 4.—Time of day (GMT + 2h) when plovers of both sexes were trapped in the nest. Bars represent numbers of trapped individuals.](image-url)
b) Nest predation

During 1991 and 1992 actual and potential predators of Kentish Plover nests included domestic dogs, foxes (Vulpes vulpes), badgers (Meles meles), weasels (Mustela nivalis), polecats (Mustela putorius), Gull-billed Terns (Gelochelidon nilotica), Common Ravens (Corvus corax) and ladder snakes (Elaphe scalaris). In other nesting seasons ocellated lizards (Ceratia lepida) and Turnstones (Arenaria interpres) have been recorded preying on eggs (J. A. Amat, pers. obs.). All the avian predators were mobbed by nesting Kentish Plovers, particularly the Gull-billed Terns (see below).

We identified nest predators in 30 nests, by recent tracks in soil and/or egg remains characteristics. Birds preyed upon 11 nests, and mammals (dogs, foxes, badgers, or polecats) on 18, and a snake took one clutch. In one nest a mammalian predator also killed the incubating female.

In 1991 predated nests survived an average of 14.3 days from clutch completion to predation (n=47); in 1992 predated nests survived on average 10.8 days (n=151). The difference between years was significant (Mann-Whitney U-test, \( U = 9.86, P = 0.0017 \)), which might indicate a greater predation pressure on nests in 1992 (see also Table 3). The survival times of predated nests were not associated or correlated with any of the variables describing the nest site (degree of cover, and distances to water and nearest neighbour). Among predated nests, survival times were longer for clutches found with three eggs than for clutches found with two eggs (means of 12.6 and 8.8 days, Mann-Whitney U-test, \( U = 10.01, P = 0.002 \)).

Success was also calculated in terms of eggs rather than clutches: it was 27.6% in 1991 (70 out of 254 eggs with known outcome hatched), and 16.1% in 1992 (89 out of 554 eggs hatched).

c) Partial predation

Partial predation (i.e. losses of one or two eggs in clutches of three) affected 39 of the three-egg clutches, and (losses of one egg) 10 of the the two-egg clutches; overall, 49 out of 288 clutches (17.0%) were reduced after our
first check. In five cases we found the missing eggs near the nests, and they were damaged. All cases of partial predation were probably due to avian predators. The 18 clutches reduced to one egg were deserted, with two exceptions where the single eggs were successfully incubated. A nest that suffered partial predation and was subsequently deserted is classified as «predated» throughout this paper (as in Table 3).

d) Replacement clutches

Kentish Plovers pairs that lost clutches usually renested together in another scrape. In 1991 we found 6 cases of replacement clutches (10.9% of 55 losing initial nests), and 36 in 1992 (22.5% of 160 nests). One case in 1991 and two cases in 1992 involved pairs whose first nests were successful, but lost their chicks when these were less than 20 days old. Among the cases in 1992 we found five pairs that produced three clutches, and one pair that produced four clutches (all unsuccessful).

The number of days between the loss of the first nest (or brood) and the initiation of a second nest was 23.8 ± 20.37 (n = 35). When the second nest was lost and the pair initiated a third nest, the mean number of days between the loss of the second nest and the initiation of the third nest was 10.8 ± 10.64 (n = 5). This difference in number of days between nesting attempts may be due to the fact that we could have missed some of the renesting attempts of early breeders. The distance moved between nest sites in the cases of replacement clutches was very variable, ranging 0-3291 m between the first and second nesting attempts (mean 467.0 ± 877.67 m, n = 36), and 8-56 m between the second and third nesting attempts (mean 35.8 ± 19.10 m, n = 5).

The body masses of females were similar between the first (41.2 ± 2.49 g) and second (42.0 ± 2.55 g) nesting attempts (Student’s paired t-test, t = 1.25, n = 34, P = 0.22), as well as between the second (42.4 ± 3.36 g) and third (41.3 ± 5.50 g) nesting attempts (Student’s paired t-test, t = 1.58, n = 4, P = 0.21). However, the body masses of males were lower in the first (42.8 ± 2.75 g) than in the second (43.7 ± 2.61) nesting attempts (Student’s paired t-test, t = 2.05, n = 32, P = 0.049). No differences were found in the body masses of males between the second (43.8 ± 2.06 g) and third (43.3 ± 2.50) nesting attempts (Student’s paired t-test, t = 0.23, n = 3, P = 0.840).

**Chicks and brood care**

The incubation period (6 nests with 3 eggs) varied from 25 to 29 days (mean 27.2 days). In a single two-egg clutch incubation lasted 24 days. From the first detectable breakage of the eggshell, hatching lasted up to 72 h. In four cases eggs with well formed embryos, but not pipped, were abandoned in the nest after the first chicks hatched. The mean number of chicks hatched per successful nest was 2.69 (70/26) in 1991 and 2.54 (89/35) in 1992.

Chick body mass at hatching varied between 5.3 and 7.6 g (mean 6.33 ± 0.56 g, n = 47). Chick mass at hatching was strongly correlated with egg mass at laying (r = 0.92, n = 19, P < 0.001). At hatching chick mass represented 64.0 to 73.8 % of the respective egg mass. Data on body mass and age in chicks of known age (n = 131 data points of 42 chicks) were fitted to the logistic curve (Ricklefs, 1983); the estimated asymptotic mass was 34.05 g, and the growth rate 0.105 g/day per each gram of body mass of the chick (r = 0.95, P < 0.001).

Chicks were highly mobile shortly after hatching, and by the day after hatching they could be seen hundreds of m, even km (in one case up to 4 km), from the nest site. Occasionally, if pursued chicks attempted to escape by swimming (from day 20). Chicks fledged around the age of 30 days.

Survival estimates for highly mobile and cryptic chicks in a complex terrain like Fuente de Piedra were basically unreliable. We observed attacks of Gull-billed Terns on ringed chicks, and also found colour rings and the corpse of a ringed chick in tern colonies. We found other four dead ringed chicks, whose causes of death were unknown, but could be due to an epizootic (three cases in 1992). We observed a male Kentish Plover repeatedly pecking a small colour ringed chick, and found such a chick dead the following day, so some cases of infanticide may occur. From late May when the water level was low, non-fledged ringed chicks foraged in
the mouths of small streams that fed the drying lake, probably because of higher concentrations of food there. Aggressive behaviour between the brood-tending adults were very frequent at such sites.

Chicks were attended and escorted by both parents in most cases well up to the second week after hatching (Fig. 6). Chicks aged three weeks, or older, were more commonly escorted by the male parent alone. The association between chicks and male parents may persist after the chicks fledge, as we once trapped a ringed male in his second nest together with one of its ringed 53-days old chick from his first nest. Care of the brood only by the female was very rare at Fuente de Piedra (Fig. 6).

Parental behaviours included brooding, alarm calls, distraction displays, and attacks on some predators as well as on conspecifics. We saw both sexes performing these behaviours. During 18 h of focal observations on 13 broods when both parents were present, we saw 55 attacks by plovers on Gull-billed Terns (one attack every 20 min). Male parents performed this behaviour more frequently than did the females (41 vs. 14 attacks on terns, \( P < 0.01 \), Wilcoxon signed ranks test). During this period we also saw 20 attacks on conspecifics, equally shared by both sexes (often the conflict was pair vs. pair). We saw on two occasions attacks of Great Grey Shrikes (\( Lanius excubitor \)) on colour ringed plover chicks. Other potential avian predators of Kentish Plover chicks were Kestrels (\( Falco tinnunculus \)) and Little Owls (\( Athene noctua \)).

Mate changes

a) Within seasons

In 1992 there were six cases in which the pairs, after losing their nests, split before initiating their second nests. In these cases the females \( (n = 5) \) or the male \( (n = 1) \), were recaptured in a new nest with a different mate.
The mean number of days between splitting of their first mates and initiation of the second nest with a new mate was 17.8 $\pm$ 5.98 for females ($n = 5$). The body masses of these females were similar in their first and second nests (42.0 $\pm$ 1.58 g vs. 41.4 $\pm$ 3.13 g, respectively, Student’s paired t-test, $t = 0.58$, $P = 0.59$).

b) Between seasons

The members of six Kentish Plover pairs that in 1991 were captured nesting together, were retrapped nesting together in 1992. Nevertheless, 11 pairs in which both members nested together in 1991, and were known to be alive in 1992, mated to a different individual in the later year.

c) Polygamy

In 1991 we recorded one case of sequential polyandry and another of sequential polygyny. In these cases was involved a Kentish Plover pair following the successful rearing of chicks of its first nesting attempt. In 1991 we also recorded a case of simultaneous polygyny, that is a male simultaneously tending two nests (see below).

In 1992 we recorded two additional cases of sequential polyandry, and three cases of sequential polygyny. All these cases occurred after the successful rearing of chicks. Moreover, we found another case in which, following the experimental removal of the female from a successful nest, the male mated to a different female.

Distances between the first and the second, polygamous nests were 1270.0 $\pm$ 1486.2 m for females ($n = 3$) and 366.5 $\pm$ 324.5 m for males ($n = 4$). In all these cases of polyandry, the females deserted the broods before the chicks fledged, and the chicks remained under the care of males until fledging. The mean number of days between the initiation of the first nest and the initiation of the second, polyandrous nests was 71.0 $\pm$ 14.73 ($n = 3$). For males, the mean number of days between the initiation of the first nest and the initiation of the second, polygynous nests was 78.3 $\pm$ 11.00 ($n = 4$). The body masses of males decreased significantly from 46.0 $\pm$ 1.83 to 42.0 $\pm$ 3.65 g ($n = 4$) between first and second polygamous nests (Student’s paired t-test, $t = 3.70$, $P = 0.034$), whereas those of females increased from 41.0 $\pm$ 6.56 to 47.0 $\pm$ 4.04 g ($n = 3$), but in this case the difference was not significant (Student’s paired t-test, $t = 3.20$, $P = 0.085$).

DISCUSSION

The local plover population

Our data on philopatry and longevity (we have recaptured a few individuals up to 9 years old, J. A. Amat, unpubl.) of the Kentish Plover population in Fuente de Piedra agree with results published from other sites in Europe (Johnson and Pineau, 1992; Jonsson, 1995) and North America (Paton, 1994). Our study is the first to report significant sexual size dimorphism in tarsal length and body mass among adult Kentish Plovers (cf. Cramp & Simmons, 1983), males being larger. In the Netherlands and southern France body mass of both sexes declined throughout the breeding season (Glutz von Blotzheim et al., 1975; Pineau, 1994), but at Fuente de Piedra we found this pattern only in males. Perhaps this could be due to a greater involvement of males in incubation duties as the season advances, since during the late nesting season males participated more frequently in diurnal incubation than during the early nesting season (see below).

There are some reports of long distance movements (> 100 km) of individuals within a breeding season in some plover populations (Székely & Lessells, 1993; Stenzel et al., 1994; Jönsson, 1995). In southern Spain, we did not find any evidence of such movements among breeding Kentish Plovers, despite our repeated search for colour ringed Kentish Plovers from Fuente de Piedra in the main breeding locality of the species in southern Spain (about 145 km WSW from Fuente de Piedra), as well as in some nearby lakes around Fuente de Piedra. The largest populations of Kentish Plovers in Europe are found in the southern Iberian Peninsula (Tucker & Heath, 1994). Probably, the saturation of breeding localities by dense populations of Kentish Plovers in southern Spain would make it more difficult for birds to move among localities to establish a nesting territory than for plovers nesting in other regions where breeding densities may be smaller.
Breeding biology

The breeding biology of Kentish Plovers at Fuente de Piedra differs in some striking ways from patterns reported from elsewhere. Most of the differences can be related to the high predation levels and the characteristics of chick predators at Fuente de Piedra. The length of the breeding season is comparable to the less extensive data reported from other sites in the Southern Palearctic, like Iraq (Glutz von Blotzheim et al., 1975). Nevertheless, the length of the breeding season at our study site varies considerably between years. This variation must influence the chances of producing replacement clutches and of rearing second broods.

Levels of nest predation (total) were as high (or higher) at Fuente de Piedra as at most sites reported in the literature (Rittinghaus, 1956; Lessells, 1984; Warriner et al., 1986; Székely, 1992; Paton, 1993), and higher in another site in the Iberian Peninsula (Ballesteros & Torre, 1993). Again, predation levels fluctuated between months and years, with a trend to increase towards the end of the breeding season. Probably the low water levels around islets and dykes in the late breeding season increased the exposure of nests to terrestrial predators. However, other factors may also play a role, as an increment in predation pressure throughout the breeding season has also been reported in another study in coastal NE Spain (Ballesteros & Torre, 1993). Variations in water levels could also account for differences in predation rates between years.

Variables measured for each nest site (nest cover and distances to water and nearest neighbour) had no detectable effect on predation rates or nest survival times. The great variety of predators at this site (reptilian, avian, mammalian; nocturnal and diurnal, visually-oriented and not) possibly precludes that a single physical feature of a nest can act as an integral defence against predation (see Colwell, 1992; Filliatre et al., 1994). In a locality with a less diverse community of nest predators, it was found that nest-site characteristics influenced nesting success (Page et al., 1985). Kentish Plovers responded to nest losses by renesting, which is a characteristic of birds subject to high levels of nest predation (Filliatre et al., 1994).

Our data indicate that most two-egg clutches could result from partial predation. During periods of reduced predation (i.e. at the start of the season in March, Table 2) the ratio of two to three-egg clutches was low (2.9%) and comparable to that reported from Hungary (Székely et al., 1994). Why was partial predation so frequent at Fuente de Piedra? We believe that predators responsible for partial predation are those that adult Kentish Plovers could attack and expel from the nest with some degree of success, like Gull-billed Terns, which from April onwards were particularly abundant at our study area. Partially predated nests in which clutch sizes were reduced to two eggs were incubated, but those nests in which clutch sizes were reduced to one egg were almost invariably deserted. Only in two cases in which partially predated clutches were reduced to one egg were such clutches incubated, and in both cases the nests were started in the late nesting season. Decisions to desert partially predated clutches seem therefore to be influenced by an interaction between clutch value and probability of renesting. The number of eggs lost was a good predictor of the value of a nest and influenced nest desertion (Armstrong & Robertson, 1988; Delehanty & Oring, 1993). Nest desertion was therefore affected by a trade-off between current reproductive investment and expected benefits of a new breeding attempt (Carlisle, 1982).

There was no evidence that the seasonal constancy of female body mass resulted from a lower maternal investment in clutches. Egg width and egg volume were larger at Fuente de Piedra than in Hungary (data from Székely et al., 1994). Female mass is higher in Hungary (Székely & Williams, 1994), so our data suggest that female plovers at Fuente de Piedra may invest more energy in eggs (in terms of the ratio clutch mass/body mass). Egg size in Hungary did not show significant differences between habitats or years (Székely, 1992). In Hungary, egg size decreased throughout the breeding season (G. Noszály & T. Székely, pers. comm.), but in Fuente de Piedra egg size increased during the season in 1991, but not in 1992. Possibly the food supply for laying females at Fuente de Piedra is higher than in Hungary. Furthermore, the food supply for Kentish Plovers in
Fuente de Piedra could improve throughout the breeding season (A. Pérez-Hurtado & J. A. Amat, unpubl.), which could explain some of the variation in egg size (see Blomqvist & Johansson, 1995)

**Parental care and mating system**

In the Kentish Plover, like in other shorebird species in which incubation is shared by both sexes, males mainly incubated at night and females during daytime (Nakazawa, 1979; Howe, 1982; Bergstrom, 1986; Warriner et al., 1986; Brunton, 1988; Paton, 1985; Thibault & McNeil, 1995). However, male Kentish Plovers occasionally also participated in diurnal incubation, especially late in the season when ambient temperatures were high and females could be heat stressed (see Ward, 1990).

At Fuente de Piedra, we have recorded some adults to have been preyed upon while incubating at nests (see above; J. A. Amat, unpubl.). Those nests in which one of the incubating adults is preyed upon are abandoned, probably because a single parent can not face incubation costs alone. Nevertheless, during the last week of incubation a single parent is able to successfully incubate the clutch (Warriner et al., 1986). During our study, we experimentally removed two males and two females from nests during the last week of incubation, and all four nests were successfully incubated by the remaining adult (J.A. Amat & R.M. Fraga, unpubl.). This ability of a single parent to incubate alone during late incubation could account for the single case of simultaneous polygyny that we recorded. In such a case, the second nest was initiated 20 days later than the first one.

Biparental care of the brood lasted longer at Fuente de Piedra than elsewhere (France: Lessells, 1984; North America: Warriner et al., 1986; Paton, 1995; Hungary: Székely & Lessells, 1993). Usually at these sites females desert the brood at the end of the first week, whereas at Fuente de Piedra they remain 20 days with the brood. Female Kentish Plovers at Fuente de Piedra perform parental activities, like alarming and brooding chicks, and also attack Gull-billed Terns (though less frequently than males) and other avian predators. We suggest that the increased maternal protection of the brood at Fuente de Piedra mainly results from an interrelationship between high predation pressure and type of predators. When the predator is small enough to be attacked by adult plovers (as is the case with most avian predators at Fuente de Piedra), and the attacks of parent plovers on predators are effective in deterring these, as is the case with Gull-billed Terns, this should select for prolonged parental care (Larsen, 1991). In our study Gull-billed Terns killed a ringed 16-day old plover chick. Perhaps, the length of stay of females with broods in Fuente de Piedra roughly corresponds to the duration of chick vulnerability to their main predators.

Proximate factors, such as length of the breeding season and levels of clutch failure, may constrain the frequency of sequential polygamy (Warriner et al., 1986; Colwell & Oring, 1988). Nest predation plays a role in reducing the frequency of second broods, because it reduces the chance of rearing the first brood, increases the frequency of renesting, and thus postpones the rearing of a second brood. As nest predation at Fuente de Piedra increased during the course of the season, by June the probability of successful second broods for females and males still attending chicks would be very small. During 1991 and 1992, when predators had free access to nests, only 7 cases of polygamy were recorded, involving 3 females and 4 males. In 1994, when many nests were protected from predators with exclosures, 10 cases of polygamy were recorded (7 females and 3 males involved), out of a total of 90 nests for which both male and female were individually marked (J. A. Amat, unpubl.). This suggests that the polygamy potential of Kentish Plovers at Fuente de Piedra is indeed limited by high nest predation levels. After controlling for the length of the breeding season and level of clutch failure, the frequency of sequential polygamy at Fuente de Piedra should be lower than in other sites, because brood desertion by one of the parents took longer at our study locality.

Desertion of Kentish Plover broods by females is much more frequent than by males (Lessells, 1984; Warriner et al., 1986; Paton, 1995; Székely & Williams, 1995; this study). This has also been found in other shorebird
species with biparental care systems (Howe, 1982; Jönsson & Alerstam, 1990; Gratto-Trevor, 1991; Whitfield & Brade, 1991; Yalden & Holland, 1992; Székely & Reynolds, 1995). Why do Kentish Plover females desert broods more frequently than males do? Confrontations of Kentish Plover parents with other adult plovers are frequent in brood rearing zones (Warriner et al., 1986; Székely & Williams, 1995; this study). Although both parents participate in brood defence against the attacks of conspecifics, male defence could be more effective than female defence. This is suggested by the fact that in the very few instances in which infanticide has been recorded in this species (Warriner et al., 1986; this study), the broods were attended by the females alone.

Females deserting broods could benefit in two ways (Myers 1981; Jönsson & Alerstam, 1990; Gratto-Trevor, 1991). First, they could gain body mass to lay second clutches. Second, even if such females do not initiate second nesting attempts, they could gain advantages derived from early initiation of plumage moult.

In conclusion, when incubation constrains time budgets (Maxon & Oring, 1980), as it may be the case in the Kentish Plover, shared parental incubation is necessary. Under these circumstances, the inability of a single adult to incubate alone might limit the frequency of simultaneously polygamous matings. The Kentish Plover, therefore, pays a cost of polygamy during the incubation stage (Walters, 1982), and to a lesser extent during the brood rearing stage.

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