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András Kosztolányi<sup>a</sup>, Sàlim Javed<sup>b</sup>, Clemens Küpper<sup>c</sup>, Innes C. Cuthill<sup>d</sup>, Abdunnasser Al Shamsi<sup>b</sup> & Tamás Székely<sup>c</sup>

<sup>a</sup> Department of Ethology, Eötvös University, Pázmány P. sétány 1/c. H-1117, Budapest, Hungary

<sup>b</sup> Environment Agency – Abu Dhabi, PO Box 45553, Abu Dhabi, UAE

<sup>c</sup> Department of Biology and Biochemistry, University of Bath, Bath, BA2 7AY, UK

<sup>d</sup> Centre for Behavioural Biology, School of Biological Sciences, University of Bristol, Woodland Road, Bristol, BS8 1UG, UK

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# Breeding ecology of Kentish Plover *Charadrius alexandrinus* in an extremely hot environment

ANDRÁS KOSZTOLÁNYI<sup>1</sup>\*, SÀLIM JAVED<sup>2</sup>, CLEMENS KÜPPER<sup>3</sup>, INNES C. CUTHILL<sup>4</sup>,  
ABDULNASSER AL SHAMSI<sup>2</sup> and TAMÁS SZÉKELY<sup>3</sup>

<sup>1</sup>Department of Ethology, Eötvös University, Pázmány P. sétány 1/c. H-1117, Budapest, Hungary,

<sup>2</sup>Environment Agency – Abu Dhabi, PO Box 45553, Abu Dhabi, UAE, <sup>3</sup>Department of Biology and Biochemistry, University of Bath, Bath BA2 7AY, UK and <sup>4</sup>Centre for Behavioural Biology, School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, UK

**Capsule** Hot environments are associated with more biparental care, high nest-site fidelity and low mate fidelity.

**Aims** To investigate the breeding ecology and parental behaviour of Kentish Plovers in an extremely hot environment. Kentish Plovers have an unusually diverse breeding system in which the frequencies of biparental, female-only and male-only care vary between populations. A common, but rarely tested, explanation for such a variation is local adaptation: birds exhibit social traits that are adaptive to their breeding environment. In particular, we investigated the effect of a hot environment on breeding success, distribution of care types, and mate and site fidelity.

**Methods** A breeding population of approximately 200 pairs of Kentish Plovers was investigated in 2005 and 2006 at Al Wathba Wetland near Abu Dhabi in the United Arab Emirates.

**Results** We found high nest-site fidelity, low mate fidelity and more biparental care in Al Wathba than in most temperate zone populations of Kentish Plovers.

**Conclusions** Our results are consistent with the argument that a harsh environment can select for biparental care. However, further studies are warranted to distinguish between alternative hypotheses for the different distribution of social behaviours of breeding populations.

## INTRODUCTION

Waders (or shorebirds; approximately 350 species) (Monroe & Sibley 1993) have a global distribution: they breed on all continents including Antarctica (del Hoyo *et al.* 1996, Kam *et al.* 2004). Successful breeding in vastly different environments such as Arctic tundra, temperate wetlands, deserts and tropical marshes requires special adaptations. These adaptations may influence fundamental aspects of birds' biology including physiology, life histories and resilience to perturbations caused by humans.

There are two fundamental reasons for collecting data on the behaviour and ecology of waders in different environments. First, waders exhibit an unusual diversity in their behaviour, ecology and life histories,

with complex phylogenetic relationships between these traits (Bókonyi *et al.* 2003, Székely *et al.* 2004, Thomas & Székely 2005, Thomas *et al.* 2007). Studies have shown that the environment often shapes these traits, although a common limitation of such comparative studies is that life history and ecological data are scanty from tropical and subtropical regions, where many waders breed. Second, to assess the status and trends of populations, we need baseline data on breeding ecology and the long-term sustainability of populations. While waders feature prominently in studies of evolutionary ecology including migration, foraging ecology and breeding systems (see reviews by del Hoyo *et al.* 1996, Kam *et al.* 2004, Thomas *et al.* 2007), collecting data on their demography is difficult, due to their low breeding densities in transient habitats, the nomadic nature of breeding adults, and the high mobility of their young (but see McCulloch 1992, Sandercock 2003, Watson *et al.* 2006, Lloyd 2008, Zefania *et al.* 2008).

\*Correspondence author. Email: andras.kosztolanyi@gmail.com

A powerful approach to investigating the influence of environment on breeding strategies is to focus on a single species that breeds under different environmental regimes, and look to see whether these different ecological conditions may evoke different social traits; for instance mating system and type of parental care. Here we focus on a widely distributed wader, Kentish Plovers *Charadrius alexandrinus*. This species has a broad geographic distribution in Eurasia from Cape Verde Islands in the west to Taiwan and Japan in the east, and they breed in open habitats in the northern hemisphere between latitudes 55° (N. Germany) and 10° (Sri Lanka). Kentish Plovers are polygamous (either by the male or the female) (Lessells 1984, Warriner *et al.* 1986, Blomqvist *et al.* 2002), and the chicks may be raised by a single parent or both parents. Kentish Plovers are one of the few bird species in which several factors have been identified that may influence whether one or both parents care for the young (Amat *et al.* 1999, Székely & Cuthill 1999, Székely *et al.* 1999, Kosztolányi *et al.* 2006). Extreme ambient environments, for example temperature extremes that may endanger the survival of offspring in the absence of intense parental care, may select for biparental care, which may induce a suite of changes in life history traits including persistence in breeding at the same site with the same mate (Lloyd 2008, Al-Rashidi *et al.* unpubl. data).

We had three objectives in this study. First, to investigate breeding strategies of Kentish Plovers in a harsh desert environment where ground surface temperature rises above 45 °C on most days (see later); this temperature is lethal for the developing embryo if it is left unattended and we expected many nests to fail without extensive parental care. Parental care and sexual selection and their relationship with the environment are controversial topics in evolutionary biology (Kokko & Jennions 2008), and empirical studies, like the one we present here, are needed to underpin (or disprove) theoretical arguments. Secondly, to protect chicks from scorching heat, both parents must cooperate to rear the young. Therefore, a high incidence of biparental care was predicted. Finally, if the breeding environment exhibits low variation across the year, one may expect pairs to stay together between years and, due to a non-migratory lifestyle, to return to their former home range; thus, both mate and site fidelity should be high. Previous studies have investigated the breeding ecology of Kentish Plovers in Europe (Germany, Rittinghaus 1961; Hungary, Székely 1991; France, Lessells 1984; Spain, Fraga &

Amat 1996; Turkey, Kosztolányi *et al.* 2006). Here we investigated Kentish Plovers in the southernmost population to date, the Arabian Peninsula. Previous accounts of Kentish Plovers in Abu Dhabi reported sightings and the occurrences of chicks and nests (P. Hellyer, S. Aspinall, pers. comm.), but no detailed study was available from any Eurasian population that breeds further south than Turkey.

## METHODS

We investigated Kentish Plovers at Al Wathba Wetland Reserve, about 40 km south-east of Abu Dhabi, United Arab Emirates (24° 15.5' N, 54° 36.2' E) in two years (2005: 23 March–23 July; 2006: 26 April–12 July). The Reserve is approximately 3.7 km × 1.9 km with total area about 450 ha; it is composed of water bodies surrounded by sand dunes. The Reserve is managed by the Environment Agency – Abu Dhabi (EAD), and the area is surrounded by a fence that excludes large terrestrial predators (see detailed description by Khan & Javed 2004).

We used standard methodology to estimate survival of nests and broods, and chick growth rates (Kosztolányi *et al.* 2006, Székely *et al.* 2008). In short, we searched for nests by observing plovers from a hide or car, or by walking through the area. For each nest, standard measurements were taken (Székely *et al.* 2008). Nests were visited at 4–5-day intervals until the age of 20 days and every day after this age to assess nest fates. The fate of the clutch was assigned to one of the following categories: 'Hatched' – at least one egg hatched; 'Predated' – the eggs were known to be depredated either by signs around the nest, by direct observations or by nest camera records (see later); 'Failed' – no eggs hatched (because the eggs were infertile or the embryo died in the egg and/or the parents deserted the nest); or 'Unknown' – the fate of the nest was not followed or the eggs disappeared, but neither predation nor hatching was confirmed. The number of nests with unknown fates are indicated in Table 1; however, these nests were excluded from the statistical analysis. We calculated Mayfield nest-survival rates and nest success (Mayfield 1975, Johnson 1979).

**Table 1.** The fate of Kentish Plover nests in Al Wathba.

Year	Hatched (%)	Predated (%)	Failed (%)	Unknown (%)	Total no. of nests
2005	23.4	43.1	12.8	20.7	188
2006	19.4	36.4	14.0	30.2	129

We set up nest camera systems to record the behaviour of parents at the nest. The system consisted of a small camera (OutdoorCam, Swann Communications Pty. Ltd.) positioned about 1 m from the nest, and a digital video recorder (MemoCam, Video Domain Technologies Ltd.) that recorded images on a memory card every 20 seconds. The camera had infrared lights for night images. To measure ambient temperature at nests observed with a camera, a thermo-probe was placed about 25 cm from the nest scrape at ground level and connected to a data logger (Tinytag, Gemini Data Loggers Ltd.) that recorded temperature every 20 seconds.

Adults were identified in the field by a unique combination of one metal and three colour rings. Downy chicks were ringed by two rings, one metal ring and a colour ring (the same colour within a family).

In 2005, broods were visited regularly after hatching, and at each visit the location of the family, the sex and number of attending parents and the number of chicks were recorded. If a parent was not present at the brood at two consecutive visits, we considered the parent as having deserted. Broods were followed until the chicks were 25 days old. For broods which hatched from unknown nests, the chicks were ringed at the first encounter, and we used their tarsus-length to estimate hatching date (see Székely & Cuthill 1999). We attempted to recapture chicks once a week to measure their left and right tarsus length (nearest 0.1 mm). Growth rate of chicks was estimated by fitting a least-squares regression for each brood, and using the slope of this regression ( $\text{mm} \times \text{day}^{-1}$ ). Tarsus growth is approximately linear in Kentish Plovers between hatching and age 25 days (Székely & Cuthill 1999).

During fieldwork whenever we encountered a colour-ringed plover we recorded its location, and noted its behaviour. We defined the home range of an individual as the convex hull of the points where the plover was observed in a given year. In home range size calculations only those birds that were observed in at least three different locations in a year were included. The distance that birds moved between years was calculated as the distance between the centroids of the two home-range polygons. For plovers with several nests in a year we calculated the between-year nest distance using their first known nest in each year.

Statistical analyses were carried out using R 2.7.1 (R Development Core Team 2008). For non-parametric data we provide the median (M), the lower quartiles (LQ) and the upper quartiles (UQ).

## RESULTS

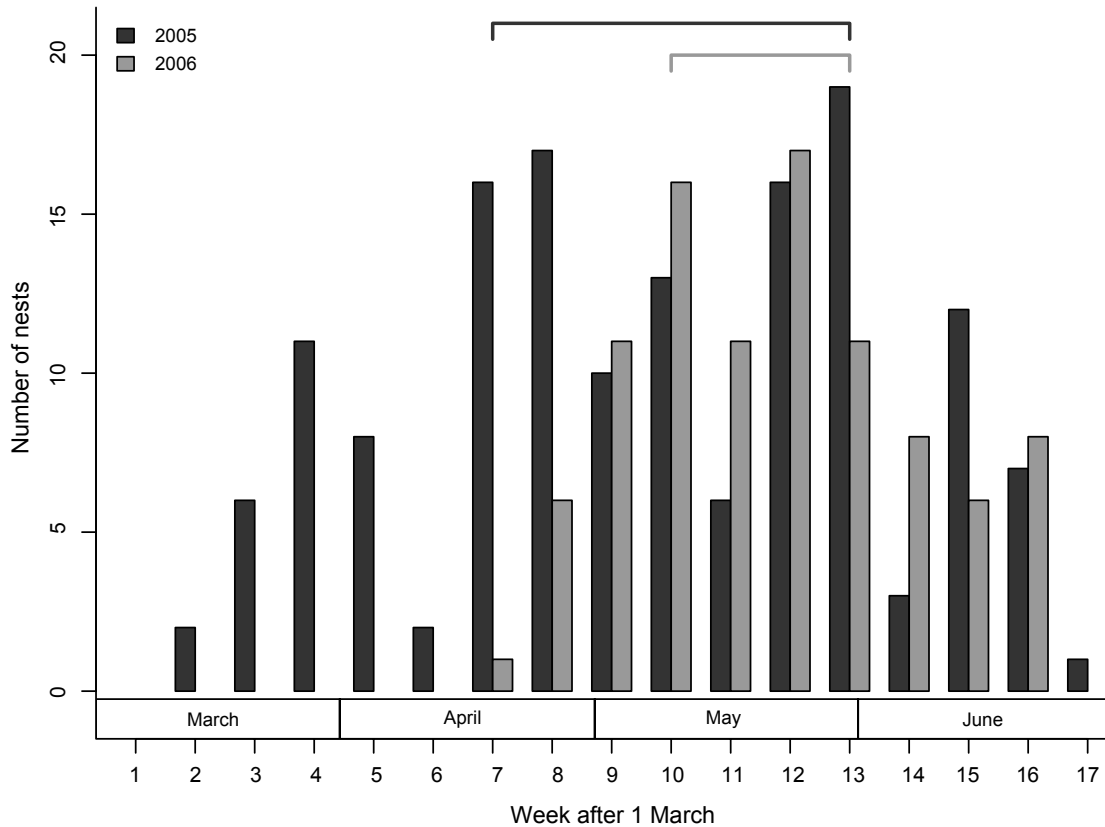
### Egg laying dates and incubation period

We found 317 nests in total in the two years. Out of 260 completed nests 163 had three eggs, 82 had two eggs and 15 had only one egg. Eggs were laid between 13 March and 24 June (2005), and 13 April and 20 June (2006). Most eggs were laid in April and May (Fig. 1). Note, however, when fieldwork started in 2005 we had already observed chicks. Based on the estimated ages of these chicks, egg laying may start as early as February, and it may last until late November, since S. Aspinall (pers. comm.) reported downy chicks from Al Wathba in December 2005.

The proportion of nests which hatched chicks was 23.4% and 19.4% in 2005 and 2006, respectively (Table 1). The fate of nests did not differ between years ( $\chi^2$  test of homogeneity for hatched, predated and failed categories,  $\chi^2 = 0.592$ ,  $df = 2$ ,  $P = 0.744$ ). The daily Mayfield survival rate of nests was  $0.94 \pm 0.0046$  (mean  $\pm$  se,  $n = 227$  nests), and the estimated nest success was 21.7% (17.0–27.6%, 95% confidence interval) for a 25-day incubation period that is similar to the apparent hatching rate.

Nest cameras identified nest predators at four nests: in two cases Grey Monitors *Varanus griseus*, in one case a Red Fox *Vulpes vulpes* and in one case a Red-wattled Lapwing *Vanellus indicus* took eggs from a Kentish Plover nest. It is unlikely that the presence of the camera and other equipment around the nest attracted the predators, because predation rate of nests where equipment was set up (24.3%) was lower than that of other nests (58.9%,  $\chi^2$  test of homogeneity,  $\chi^2 = 13.681$ ,  $df = 1$ ,  $P < 0.001$ ,  $n = 239$ ). We found footprints of Grey Monitors around several predated nests. In many cases, however, the predator(s) did not leave footprints so we could not identify them. Nests that hatched tended to be laid earlier (64.5 (50.5–81.0) days after 1 March [M (LQ–UQ)],  $n = 68$  nests) than unhatched (predated or failed) nests (71 (53–86) days after 1 March,  $n = 130$  nests, Mann–Whitney test,  $W = 3764.5$ ,  $P = 0.087$ ).

We recorded the behaviour of parents for 1–3 days using camera systems ( $n = 28$  nests). At each nest both parents incubated the eggs. The daily maximum ground temperature recorded at these nests was  $> 45^\circ\text{C}$  in 85.9% of the cases ( $n = 28$  nests and 73 days recorded between 12 April and 9 July). The length of the incubation period was 25 (24–25) days ( $n = 7$  hatched nests which were found before clutch completion).

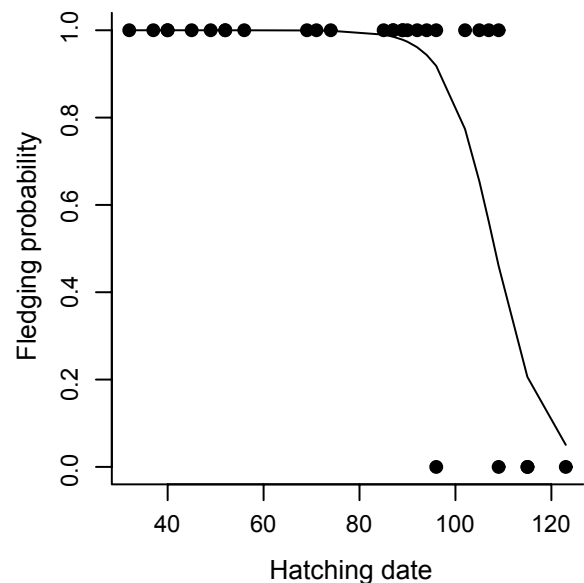


**Figure 1.** Egg-laying season of Kentish Plovers at Al Wathba. The brackets over the bars represent interquartile ranges for 2005 and 2006 separately.

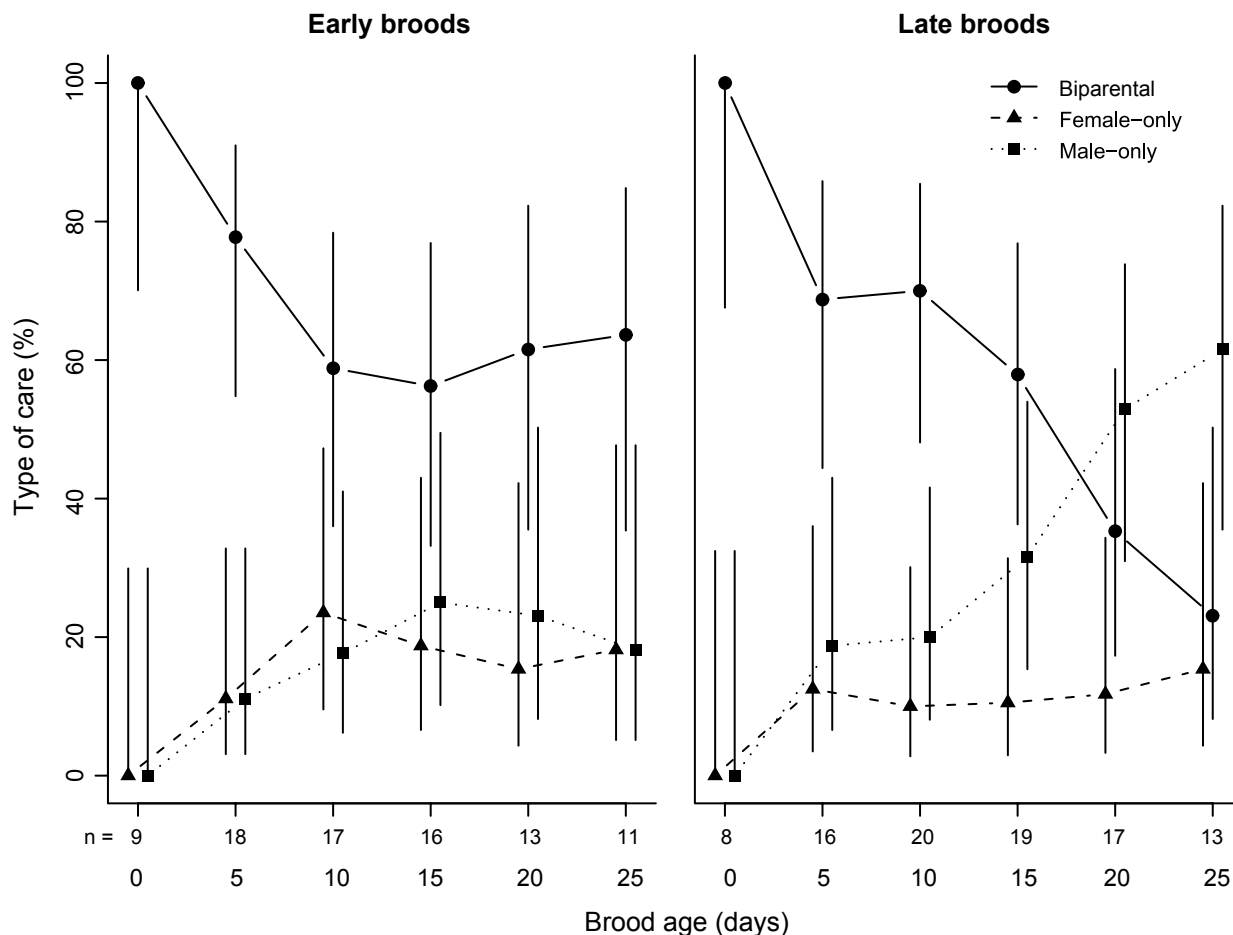
### Brood-rearing period

In 2005, 30 broods (15 hatched from known nests and 15 hatched from unknown nests) were checked regularly until the age of 25 days or until all chicks perished. Twenty five of these families fledged at least one chick successfully, and the probability of fledging decreased during the breeding season (Fig. 2; generalized linear model with binomial error,  $B = -0.20 \pm 0.09$ ,  $P = 0.034$ ). Tarsus growth of chicks was  $0.42 \pm 0.03 \text{ mm} \times \text{day}^{-1}$  (mean  $\pm$  se;  $n = 30$  broods), and chicks hatched later in the season grew faster than chicks hatched earlier (least-squares regression,  $B = 3.50 \times 10^{-3} \pm 1.18 \times 10^{-3} \text{ mm} \times \text{day}^{-2}$ ,  $P = 0.006$ ).

Biparental brood care, male-only brood care and female-only brood care were all observed in Al Wathba, and the distribution of care types tended to change with both hatching date and brood age (Fig. 3). We observed fifteen female and five male desertions, whereas in ten families both parents stayed with the chicks until the age of 25 days. Male desertion occurred 5.5 (3.5–5.5) days after hatching, whereas



**Figure 2.** The probability of fledging of Kentish Plover broods in relation to hatching date at Al Wathba in 2005. The line indicates fitted values of a generalized linear model with binomial error (see text for details); hatching date is given as number of days since 1 March.



**Figure 3.** The distribution of care types over 0–25 days of brood age in Kentish Plover broods at Al Wathba in 2005. The broods were divided into early and late broods according to the median hatching date (early broods  $n = 27$ ; late broods  $n = 26$ ); the vertical bars represent 95% binomial confidence limits.

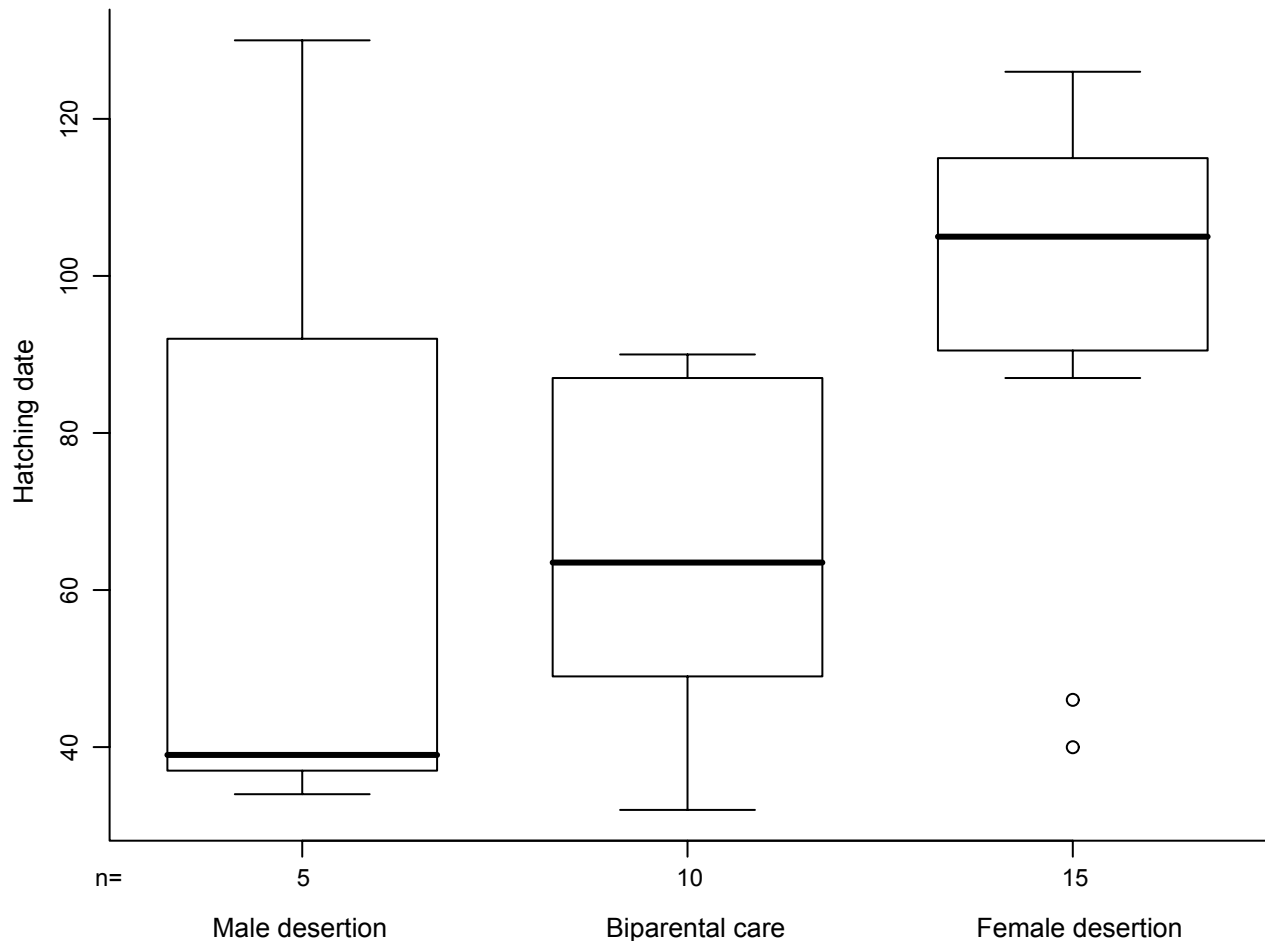
female desertion occurred 12.5 (4.3–17.5) days after hatching (Mann–Whitney test,  $W = 52$ ,  $P = 0.221$ ). Consistent with the changes in the distribution of care types, male desertion was more likely to occur in early broods (Fig. 4, Kruskal–Wallis test,  $\chi^2 = 8.850$ ,  $df = 2$ ,  $P = 0.012$ ). We observed five cases of sequential polygamy out of seven males and ten females that bred several times with known mates in a breeding season: one male in 2005 and four females (two in 2005 and two in 2006) re-nested with a different mate within the same breeding season. The polygynous male was tending alone two 22-day-old chicks from his first nest on 29 April and his first mate was seen with an unringed male on 28 April. The male re-nested with an unringed female on 7 June. The first mate of this polygynous male re-nested with an unringed male on 21 May. The other polyandrous female in 2005 deserted her first brood on 24 April

when the chicks were 14 days old, and laid a new clutch with an unringed male around 20 May. One polyandrous female in 2006 remated with a ringed male (her previous mate in 2005) after her first clutch was predated, however, her first mate was still alive and present in Al Wathba. The other polyandrous female in 2006 deserted her first brood on 27 May when the chicks were 14 days old, and then laid a new clutch with an unringed male on 5 June.

### Mate fidelity and site fidelity

Both parents were ringed in 99 pairs in 2005. Out of these, the mates of 16 males and 12 females were identified in 2006. Six males (37.5%) out of the 16, and six females (50.0%) out of the 12 re-mated with the same bird in the next year (two out of these six females, however, had two mates in one of the years).





**Figure 4.** Hatching date of broods deserted by the male, the female or neither parent at Al Wathba in 2005. Hatching date is given as number of days since 1 March.

One hundred and forty seven colour-ringed adults were observed at the study site in 2006 out of 223 adults that were marked in 2005. The returning rate of males (70.0%, 77 out of 110) did not differ from that of females (61.9%, 70 out of 113;  $\chi^2$  test of homogeneity,  $\chi^2 = 1.271$ ,  $df = 1$ ,  $P = 0.260$ ).

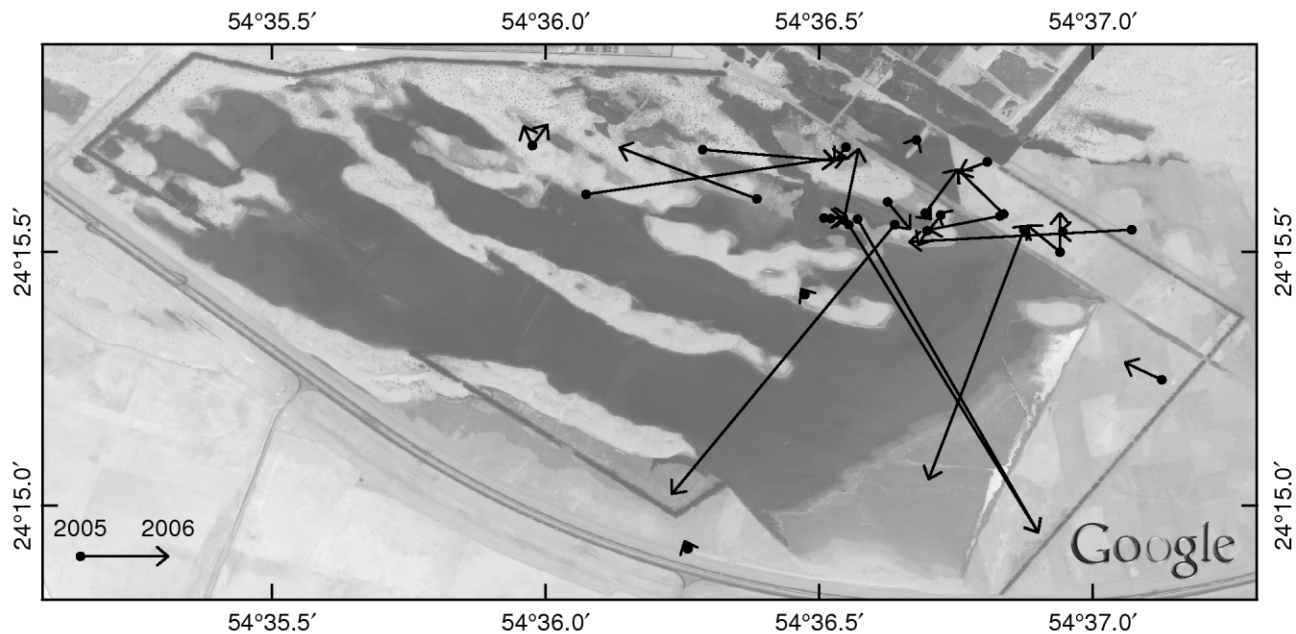
Females tended to move larger distances between years than males, although the home ranges of sexes were not different (Table 2). Plovers observed in both years tended to have smaller home ranges in 2005 (1.50

(0.19–4.75) ha) than in 2006 (2.30 (0.49–8.11) ha) (Wilcoxon matched-pairs test,  $V = 305$ ,  $n = 42$ ,  $P = 0.068$ ). This change is largely due to males that increased their home ranges by 2.25 (–0.11–9.05) ha (Wilcoxon signed rank test,  $V = 47$ ,  $n = 21$ ,  $P = 0.016$ ), whereas females' home range did not change (–2.05–2.15) ha,  $V = 117$ ,  $n = 21$ ,  $P = 0.973$ ).

We identified the nests of 38 adults in 2006 that were colour ringed in 2005. The locations of nests in 2005 were known for 34 out of 38 plovers, while the

**Table 2.** Home-range sizes and distances between home ranges of adult Kentish Plovers in Al Wathba (median, lower quartile–upper quartile;  $n$  refers to the number of adult males or females).

	Male	Female	Mann-Whitney test between males and females
Home ranges in 2005 (ha)	2.11, 0.20–4.85 $n = 54$	2.26, 0.59–6.71 $n = 56$	$W = 1354$ , $P = 0.346$
Home ranges in 2006 (ha)	3.49, 0.71–8.29 $n = 51$	1.83, 0.40–7.20 $n = 49$	$W = 1366.5$ , $P = 0.422$
Distance between home ranges (m)	245, 140–505 $n = 77$	330, 176–598 $n = 70$	$W = 2990$ , $P = 0.253$



**Figure 5.** The location of nests of individually marked Kentish Plovers that bred in both 2005 and 2006. (Plovers  $n = 34$ ; arrows  $n = 30$ ; four pairs re-nested together.) (Background image created using Google Maps™ mapping service.)

remaining four plovers were caught when they were tending the chicks, and thus their nest location was unknown (Fig. 5). The distance between nests in the two years was 92 (30–263) m. The between-year nest distances of females (139 (70–688) m,  $n = 13$ ) was not different from that of males (70 (28–216) m,  $n = 21$ ) (Mann–Whitney test,  $W = 175$ ,  $P = 0.178$ ).

## DISCUSSION

Our study of the southernmost breeding population of Kentish Plovers to date, found different behaviour and ecology between the temperate zone and the Al Wathba populations. The breeding season is almost continuous in Al Wathba. However, there is a peak period in April and May. A presumed seasonal variation in food supply may explain why late-hatched chicks grew faster than earlier ones: this is an unexpected result since in Turkey, where breeding is limited to 4 months, late-hatched chicks grow more slowly than early-hatched ones (Székely & Cuthill 1999).

We found four major results. First, nest survival was low, especially given that the site is surrounded by a fence that was intended to exclude many terrestrial predators including foxes and stray dogs. Indeed, we found no evidence that these carnivores would take substantial numbers of eggs. A common nest predator, however, was the Grey Monitor, a native lizard in the Arabian Desert.

We argue that the lizards were unusually abundant at Al Wathba for two reasons. First, Al Wathba and its breeding birds attracted predatory lizards from surrounding desert habitats, an effect we call the 'honey-pot'. Secondly, lizards are not persecuted inside the reserve – neither by humans nor by their natural competitors, so their populations can increase uncontrolled.

Our second major result was that survival of both nests and chicks declined over the breeding season, a common result that has been observed in Spain and Turkey (Fraga & Amat 1996, Kosztolányi *et al.* 2007). This is a well-known feature occurring in many temperate zone species: it may be due to increased predation rate as the season progresses, or to declining quality of birds that decide to breed later.

Thirdly, we recorded all three types of brood care (biparental, male-only, female-only) that occur in Kentish Plovers, although biparental care was more common than in other temperate zone populations (9.1% and 13.6% of 17+-day-old broods in Hungary and France, respectively; Lessells 1984, Székely & Lessells 1993). The high frequency of biparental care suggests that an extreme environment, such as in the Arabian Desert, may favour shared brood care. Chicks are often brooded and shaded in Al Wathba and, to avoid overheating, shifting care between parents is a convenient way of increasing chick survival. Note, however, that early in the breeding season the frequency of male-only care was comparable to the frequency of female-only care: this is unusual, because in



all populations that have been studied, including Snowy Plovers *Charadrius alexandrinus nivosus* (Warriner *et al.* 1986), male-only brood care is more common than female-only care. This suggests that in the Al Wathba population, the mating opportunities are biased toward males early in the breeding season, perhaps due to a female-biased adult sex ratio.

Finally, we found high site fidelity, as one may expect, given that Al Wathba is surrounded by desert and nesting opportunities are limited. In spite of high site fidelity, divorce between pairs was common, suggesting that site fidelity does not necessarily imply high mate fidelity. Therefore, a general relationship predicted by life history theory between high adult survival, site fidelity and low divorce (Lloyd 2008), can be modulated by social selection. For instance, unlike many temperate and southern hemisphere plovers (Ringed Plover *Charadrius hiaticula*, White-fronted Plover *Charadrius marginatus*) Kentish Plovers do not defend territories around their nest, and this flexibility in breeding dispersal may facilitate mate change.

In conclusion, our study provided fundamental data on the breeding ecology of a Kentish Plover population in the Persian Gulf. We show that features of this population (for example, nest survival, biparental care of the eggs, and a bias toward female desertion) are similar to temperate zone populations, whereas other features (high site fidelity, high frequency of biparental care) are distinct. We speculate that some of these differences are due to the extreme hot environment and/or high breeding density and/or high predation pressure (cf. Amat *et al.* 1999, Kosztolányi *et al.* 2006). Further understanding of Kentish Plover breeding ecology in Al Wathba requires continued monitoring of individually marked plovers.

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