THE ROYAL SOCIETY

doi 10.1098/rspb.2000.1265

Brood desertion by female shorebirds: a test of the differential parental capacity hypothesis on Kentish plovers

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The aim of this study was to examine whether the energetic costs of reproduction explain offspring desertion by female shorebirds, as is suggested by the differential parental capacity hypothesis. A prediction of the hypothesis is that, in species with biparental incubation in which females desert from brood care after hatching, the body condition of females should decline after laying to a point at which their body reserves are too low for continuing parental care. We tested this prediction on Kentish plovers (*Charadrius alexandrinus*) in which both sexes incubate but the females desert from brood care before the chicks fledge. We found no changes in either the body masses or body compositions of both individual male and female plovers from early incubation and throughout early chick rearing. Furthermore, the timing of brood desertion by females was not affected by their body condition. Neither did we find gender differences in the energetic costs of incubation. There were no differences in the timing of brood desertion between experimental and control females in an experiment in which we lengthened or shortened the duration of incubation by one week. These results indicate that energetic costs do not explain offspring desertion by female Kentish plovers and that the needs of chicks for parental care rather than cumulative investment by females is what determines the timing of brood desertion.

Keywords: brood desertion; parental care; body condition; incubation costs

1. INTRODUCTION

Desertion of offspring care by parents is widespread among birds. Although desertion by females is less frequent than that by males, offspring desertion by females is particularly common in some groups of birds such as shorebirds. Several hypotheses have been formulated to account for offspring desertion (reviewed in Székely *et al*. 1996), some of which have been specifically proposed for shorebirds (Erckmann 1983; Lenington 1984). These hypotheses are based on life-history theory so there may be trade-offs in the allocation of effort between different phases of a reproductive attempt (Heaney & Monaghan 1996). It is assumed that parental care may deteriorate the physical condition of adults and may even have survival costs (Askenmo 1979; Nur 1984; Owens & Bennett 1994). Poor physical condition of adults because of reproductive activities may be one of the factors leading to offspring desertion (Winkler & Wilkinson 1988; Clutton-Brock 1991). This could be particularly evident in female shorebirds because, as they lay some of the largest avian eggs in relation to their body size (Rahn *et al*. 1975), laying may have a detrimental effect on their physical condition. Female birds do indeed lose mass during breeding (Moreno 1989), which has been considered as an indication of stress (Drent & Daan 1980; but see Merkle & Barclay 1996).

Shorebirds have exceptional diversity in their mating and parental behaviour and much of this diversity is still not understood. Erckmann (1983) proposed the differential parental capacity hypothesis for explaining offspring desertion in shorebirds. According to this hypothesis, (i) laying may not stress females to the point that they cannot incubate but, as a consequence of laying costs, females may be less able to assume all parental care than males if deserted, and (ii) females have a higher cumulative reproductive effort than males at the onset of incubation and this difference in expenditure results in a differential effect on physiological capacity, an indication of which would be a depletion of nutrient reserves during incubation (Erckmann 1983). The first prediction of this hypothesis was tested by experimentally removing either males or females from nests (Erckmann 1983; Brunton 1988). It was found that the time from mate removal until nest abandonment was shorter for females than for males and this was considered as support for the differential parental capacity hypothesis (Erckmann 1983). However, for this type of experiment to be meaningful, all other things should have been equal, but whether this was the case was not clear. For instance, there was no control for stage of incubation, which may affect incubation persistence. Both sexes in Kentish plovers (*Charadrius alexandrinus*) continue incubation if they are deserted by their mates during the last week of incubation, but abandon their nests if deserted earlier (Warriner *et al*. 1986). After experimental removal of two male and two female Kentish plovers during the last week of incubation, all four nests were successfully incubated by the remaining adult (Fraga & Amat 1996). Therefore, without more information on other factors that affect

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Received 18 April 2000 *Accepted* 27 July 2000

incubation persistence, the results of the mate removal experiments cannot be adequately assessed.

The second prediction is critical to supporting the hypothesis but, to the authors' knowledge, it has not yet been tested. Although there is evidence that laying *per se* has little effect on lipid or protein reserves in shorebirds (Soloviev & Tomkovich 1997), incubation may be a costly activity (Piersma & Morrison 1994; Heaney & Monaghan 1996). Erckmann (1983) suggested that any difference in females for withstanding stress after laying should stem from a subtle degradation of physiological condition through time. If this is correct, we would expect that the body condition of females will deteriorate throughout incubation and, therefore, that females will desert because their body reserves are too low for continuing parental care after hatching.

Erckmann (1983) found inconsistent evidence for the differential parental capacity hypothesis in his review and called for additional evaluations of the hypothesis. In this paper, we present the results of a field study testing this hypothesis on Kentish plovers. Incubation is biparental in this species and lasts 27 days (range 22–32 days) (Rittinghaus 1956; Warriner *et al*. 1986). Between 91 and 98% of the broods are deserted by either parent when the chicks are seven to 20 days old (i.e. before fledging), although female desertion is much more frequent (82–84%) than male desertion (9–14%) (Székely & Lessells 1993; Amat *et al*. 1999). We tested the following predictions.

(i) If the energetic costs of laying act as a burden throughout incubation, then females may lose more body condition than males from early incubation and throughout chick rearing. In line with this, there will be a positive relationship between the body condition of females and their timing of brood desertion.

(ii) The field metabolic rates (FMRs) of incubating females may be higher than those of incubating males and this may lead to brood desertion by females if their FMR reaches a point (i.e. four to five times their basal metabolic rate (BMR)) above which their body condition and survival are compromised (Drent & Daan 1980).

(iii) The duration of brood care by females may be inversely related to that of the incubation period.

These predictions were tested observationally (i and ii) and experimentally (iii).

2. METHODS

(a) *Study site and birds*

The study was carried out at Fuente de Piedra Lake in southern Spain as described in Amat *et al*. (1999). The plovers were captured, measured (culmen, tarsus and wing lengths) and their body masses recorded following the procedures in Amat *et al*. (1999). Each bird was individually marked with combinations of metal and colour rings. The plovers were sexed based on their dimorphic plumage. We obtained a measure of structural body size using the first principal component scores of a principal component analysis of the three linear measurements. Body condition was estimated as the residuals of a regression of body masses on those first principal component scores.

(b) *Body reserves*

In order to determine whether there were changes in the body reserves of individual plovers throughout the breeding cycle, we used the total body electrical conductivity (TOBEC) body condition technique using an EM-Scan SA-2 Small Body Composition Analyzer (EM-Scan, Springfield, IL, USA). Because the electrical conductivity of lipids is very low, TOBEC measurements are mainly determined by lean mass (Walsberg 1988). In 1996, we captured the same adults at nests during both the first and fourth weeks of incubation and again when accompanying broods of two to six days old (i.e. before desertion by any adult). After capture, adults were transported to a field station where TOBEC measurements were made within 1 h of capture. In order to assure that nests were not left unattended after the removal of adults, we captured males at sunrise and females at sunset since incubation shifts at this time are very predictable, and males generally incubate during the night and females during the day (Fraga & Amat 1996). In addition, this procedure allowed us to control for daily variations in body mass. Chicks were also transported to the field station with their parents and released at the site of capture once TOBEC measurements had been made. Adults with chicks were captured in the early morning or late afternoon. All nests and broods that had adults that were used for TOBEC measurements had three eggs or three chicks.

The birds were docile when handled and were immobilized using a cotton wrap with Velcro fasteners (Lyons & Haig 1995). Individuals were placed on their backs on the centre of a Plexiglass tray provided by the manufacturer. The mean of five scans was used as a TOBEC index for each individual. Birds were removed from the apparatus after each scan and reinserted for the next one. Neither aluminium nor plastic colour rings had a detectable effect on conductivity and were not removed from birds when making TOBEC estimates. However, another type of metal ring had effects on conductivity and, in such cases, the metal rings were removed from birds before making TOBEC estimates. As salt water may affect conductivity readings (Scott *et al*. 1991), in order to minimize the effects of salt we removed mud from birds' legs before TOBEC estimates. The apparatus was calibrated prior to each session of TOBEC measurements.

The use of the TOBEC technique in estimating the body fat-free mass of live animals requires a calibration equation for each species, for which it is necessary to sacrifice individuals. We did not do this for legal (the Kentish plover is protected in the European Union) and ethical reasons. Therefore, we used the values provided by the apparatus as arbitrary estimates of fat-free mass levels. These values were appropriate for our purposes since the comparisons were made at the individual level and we were interested in documenting the qualitative dynamics of the body reserves of the plovers rather than the specific quantity of fat or body protein mobilized during the breeding cycle. Thus, if there were no differences in TOBEC values but there were differences in body masses during different phases of the breeding cycle, such differences would be due to the amount of body fat. Conversely, if there were changes in TOBEC readings but not in body mass, this would indicate changes in lean mass. The aim of using concurrent variations in TOBEC readings and body mass in determining variations in body fat is not possible as such variations could be accounted for by variations in lean mass; however, this was not the case in the present study (see § 3 and table 1). As the same individuals were used on different occasions, in order to analyse whether there were changes in body composition from early incubation throughout chick rearing we used ANOVA for repeated measurements.

(c) *Field metabolic rates*

We initially applied the two-sample method for measuring FMRs in incubating Kentish plovers (Speakman 1997). However, pilot experiments performed on four birds revealed that this protocol appeared to be too stressful for the animals as the birds significantly lost body mass between the taking of the initial (mean ± s.d. body mass = 41.2 ± 2.26 g) ($n = 4$) and final samples (mean ± s.d. body mass = 37.4 ± 2.23 g) (paired *t*-test, $t = 13.33$ and $p < 0.001$). Therefore, we applied the single-sample method in all birds during the breeding seasons of 1998 and 1999 (Webster & Weathers 1989). This protocol appeared to be less harmful as average body masses at the first (41.2 ± 3.95 g) and second captures (40.7 ± 4.07 g) did not differ significantly (paired *t*-test, $t = 1.59$, $n = 15$ and $p = 0.135$).

Upon capture on the nest, birds were weighed with a portable Sartorius balance to the nearest 0.1 g and a dose of 0.21–0.36 ml doubly labelled water (DLW) was injected intraperitoneally and the birds were then released. The dose was administered with a 0.5 ml calibrated insulin syringe which enabled us to determine the dose for each bird exactly. Each bird was recaptured after 24–48 h, its body mass was determined again and a small blood sample (six microcapillary tubes each filled with 15 μl blood) taken after puncturing the brachial vein. The microcapillary tubes were immediately flame sealed with a propane torch. All samples were stored at 5 °C until triplicate analysis at the Centre for Isotope Research, The Netherlands (for details, see Visser & Schekkerman 1999).

Blood samples were taken from three animals in order to determine the population-specific natural abundances of ^{2}H (−13.4% relative to standard mean ocean water (V-SMOW)) (s.d. = 2.27) and ^{18}O (+1.7% relative to V-SMOW) (s.d. = 1.05). In addition, the same DLW mixture was injected intraperitoneally into 11 control birds. A blood sample was taken 1 h after injection in these birds (assuming that an equilibration period of 1 h would be sufficient) (see Speakman 1997). These samples were also analysed in order to determine the ratio of the ^{18}O (relative to the background) and ^{2}H enrichments (relative to the background) for this specific DLW mixture ($^{18}O_{I}/^{2}H_{I}$, dimensionless). The $^{18}O_{I}/^{2}H_{I}$ value was found to be 0.1686 (s.d. = 0.00399). The average percentage of body water during the incubation period was found to be 66.2% (s.d. = 0.67) ($n = 4$ birds from the pilot experiments with the value based on isotope dilution).

The rate of CO$_2$ production (rCO$_2$, l day^{-1}) was calculated for each measurement with Speakman's (1997) equation (7.17), which corrects for the fractionation effects of heavy isotopes.

$$
r\mathrm{CO}_2 = 22.4 \times \{(N/2.078) \times (L/t) \times (\ln[^{18}\mathrm{O}_\mathrm{I}/^{2}\mathrm{H}_\mathrm{I}] - \ln[^{18}\mathrm{O}_\mathrm{F}/^{2}\mathrm{H}_\mathrm{F}]) - (0.0062 \times N \times (L/t) \times \ln[^{2}\mathrm{H}_\mathrm{I}/^{2}\mathrm{H}_\mathrm{F}])\}, \quad (1)
$$

where N represents the average size of the body water pool (moles) as calculated from the body mass and the body water percentage of 66.2 (see above) and t is the time in days between equilibration of the DLW dose and the taking of the final sample. A value of 0.1686 was used for all birds for the $^{18}O_{I}/^{2}H_{I}$ ratio (see above). The $^{18}O_{F}/^{2}H_{F}$ ratio was calculated on the basis of the individual-specific sample taken at recapture of the bird and the population-specific background values for ^{2}H and ^{18}O. The value of 22.4 in the equation represents the conversion of moles to litres. Finally, the FMR (in kJ day^{-1}) was calculated from the rate of CO$_2$ production by applying an energy equivalent of 27.33 kJ l^{-1}, as recommended by Gessaman & Nagy (1988) for a diet rich in protein and fat.

(d) *Duration of brood care by females*

In order to determine whether incubation duration affects the duration of brood care by females we performed an experiment in 1999. We selected 15 pairs of nests with clutch sizes of three eggs (the modal clutch size), with the nests in each pair differing in laying dates by six to eight days. Shortly before hatching of the earliest nest of each pair, we swapped the complete clutch of such nests with the clutch of the other nest in the same pair. Thus, we created experimental nests in which incubation was shortened by approximately one week (hereafter S nests) and other nests in which incubation was lengthened by approximately one week (hereafter L nests). Another 15 nests with three-egg clutches in which incubation duration was not altered served as controls. The laying date of each control nest was intermediate between those of the corresponding pairs of experimental nests. Ideally, we should also have chosen pairs of control nests and exchanged clutches between them but, due to limited population size, there were not enough nests available. Nests were protected from avian predators and medium-sized ground predators (e.g. red foxes *Vulpes vulpes*) with circular enclosures (Amat *et al.* 1999). The final sample sizes for statistical analyses in each category differed because all three eggs did not hatch in all nests and such broods were discarded or the nests were depredated or deserted before hatching.

After hatching, we relocated broods every one to three days and checked the number and sex of adults accompanying them. We relocated broods until one of the adults deserted from brood care or the chicks fledged. We determined brood desertion by adults following the procedures in Amat *et al.* (1999).

We also determined the timing of brood desertion by females during 1991–1998 in order to relate it to female body condition during incubation.

Statistical analyses were conducted using SYSTAT (Wilkinson 1990). We estimated the power of a test using GPOWER (Faul & Erdfelder 1992). The data were inspected for normality and homoscedasticity (Sokal & Rohlf 1981). Unless stated otherwise, mean values are presented with ±1 s.d.

3. RESULTS

(a) *Does breeding affect the body condition of plovers?*

We made TOBEC measurements for ten individual males and ten individual females during early incubation, late incubation and when they were caring for chicks of two to six days old (table 1). There were no significant differences in TOBEC readings between the sexes during those breeding phases (ANOVA for repeated measures, $F = 0.82$, d.f. = 1,18 and $p = 0.377$). Similarly, there were no differences between breeding phases for individual plovers ($F = 1.50$, d.f. = 2,36 and $p = 0.237$), nor was the sex × breeding phase interaction significant ($F = 0.31$, d.f. = 1,18 and $p = 0.587$). The statistical power of this ANOVA was high ($\beta = 0.77$ at $\alpha = 0.05$).

A similar analysis on the data of body masses also yielded similar results when comparing both sexes ($F = 0.60$, d.f. = 1,18 and $p = 0.450$). In this case, there were also no significant differences between breeding phases for individual plovers ($F = 1.92$, d.f. = 2,36 and $p = 0.161$) and the body mass × sex interaction was also non-significant ($F = 0.52$, d.f. = 2,36 and $p = 0.598$). What these results indicate is that there are no changes in the composition of body reserves of Kentish plovers from

Table 1. *Mean values (± s.e.) of TOBEC measurements and body masses of ten individual male and ten individual female Kentish plovers during the first and fourth weeks of incubation and when caring for chicks of two to six days old*

(Differences between the sexes in each breeding phase were tested with Student's *t*-tests.)

	first week	fourth week	chicks
TOBEC			
males	38.9 ± 0.97	39.7 ± 1.22	37.3 ± 0.70
females	40.6 ± 1.60	40.0 ± 1.73	39.9 ± 1.66
t-test	0.880	0.170	1.460
p-value of *t*-test	0.395	0.865	0.169
body mass (g)			
males	39.1 ± 0.79	39.7 ± 1.00	38.1 ± 0.52
females	40.4 ± 1.44	39.9 ± 0.71	39.3 ± 0.96
t-test	0.790	0.110	1.080
p-value of *t*-test	0.442	0.911	0.297

early incubation through chick rearing at both individual and gender levels. In addition, there were also no differences between males and females in either TOBEC measurements or in body masses during each of the breeding phases (table 1).

A prediction of the differential parental capacity hypothesis is that females in lower body condition should desert their broods sooner. However, we did not find such a relationship (figure 1) ($r = 0.02$, $n = 35$ individual females and $p = 0.890$).

(b) *Are there sex-related differences in field metabolic rates during incubation?*

The FMRs of incubating Kentish plovers were similar in males (100.4 ± 10.31 kJ day^{-1}) ($n = 6$, $t = 0.61$ and $p = 0.553$) and females (106.3 ± 21.85 kJ day^{-1}) ($n = 9$). In addition, the differences in mass-specific daily energy expenditure between females (2.58 ± 0.60 kJ day^{-1}g) ($n = 9$) and males (2.51 ± 0.26 kJ day^{-1}g) ($n = 6$) were similar ($t = 0.245$ and $p = 0.810$). We estimated that these birds operated at around 2.5 times BMR using Kersten & Piersma's (1987) equation.

(c) *Does the length of the incubation period affect the timing of female desertion?*

There were no differences in the body masses of females in S (41.8 ± 2.91 g) ($n = 15$), L (42.5 ± 2.16 g) ($n = 15$) and control nests (42.9 ± 2.92 g) ($n = 15$) (ANOVA, $F = 0.70$, d.f. = 2,42 and $p = 0.504$). Females in L nests incubated longer (33.5 ± 1.75 days) ($n = 11$) than females in control nests (27.2 ± 1.64 days) ($n = 13$), who in turn incubated longer than females in S nests (19.8 ± 1.34 days) ($n = 13$). The differences in the duration of incubation between nest categories were highly significant (ANOVA, $F = 226.4$, d.f. = 2,34 and $p < 0.001$).

The duration of chick care by experimental, female Kentish plovers from either S or L nests was similar to that of control females (figure 2) (ANOVA, $F = 0.22$, d.f. = 2,34 and $p = 0.805$). This does not support the prediction that females for which incubation was longer should desert their broods sooner.

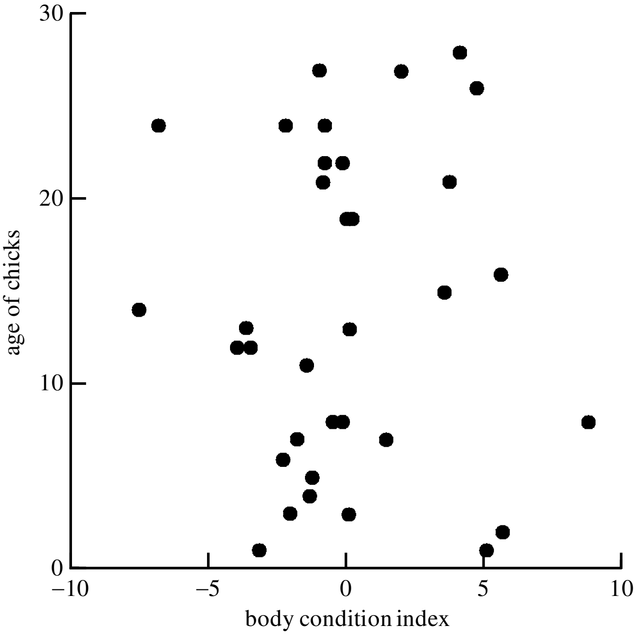

Figure 1. Relationship between the age at which Kentish plover chicks were deserted by females and the body condition of females during incubation. The index of body condition was obtained as the residuals from a regression of body mass on a measure of structural body size, expressed as first principal component scores from a principal components analysis of culmen, tarsus and wing lengths.

4. DISCUSSION

Some studies have shown that, in particular with seabirds, the body condition of breeding adults affects their reproductive performance and that it is indeed a decline in body mass during incubation that causes nest desertion (Ancel *et al.* 1998; Barbraud & Chastel 1999). However, successful breeding in seabirds is conditional on the presence of both parents during the whole dependence period of offspring because, if one parent deserts, the remaining adult cannot usually sustain the requirements of the offspring. In contrast, in other species the presence of both parents during the whole dependence period of chicks is facultative for successful breeding (Beissinger & Snyder 1987; Fujioka 1989). Erckmann (1983) tried to explain offspring desertion by female shorebirds as being a result of the energetic limitations imposed on breeding females by the costs of reproduction. According to his hypothesis, females should desert at any point in the breeding cycle at which they reach a

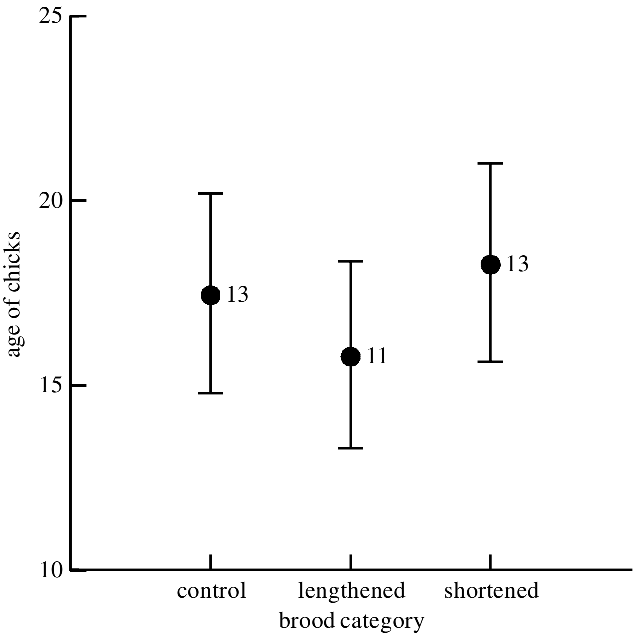

Figure 2. Mean age (± 1 s.e.) at which Kentish plover broods were deserted by females whose incubation was experimentally lengthened or shortened by a week and in control broods in which the duration of incubation was not altered. Sample sizes are shown next to points.

threshold of body condition that compromises their survival. This has been shown to occur in some female raptors (Kelly & Kennedy 1993). However, our study on the Kentish plover indicates that brood desertion by females in this species cannot be accounted for by the differential parental capacity hypothesis as formulated in energetic terms, since our data indicate that breeding Kentish plovers sustain metabolic rates without losing body mass or compromising their body condition.

As chicks grow older, they require less brooding, are less vulnerable to predators and have greater foraging skills (Pienkowski 1984). This may make the contribution of two parents for offspring survival unnecessary at a given point in the developmental period of chicks. Differences between the parents at the time at which such a point is reached would explain which parent should desert first from parental care. In a study on Kentish plovers, Székely & Cuthill (1999) found that there were no differences in chick survival between nests tended by males and females from which their mates were experimentally removed at hatching. However, another experimental study on this species showed that broods tended by males survived better than those tended by females (Székely 1996) and the more frequent desertion of females from brood care than males has been related to gender behavioural differences in the capacity to provide parental care (Oring 1986; Fraga & Amat 1996). Indeed, in some shorebird species, including the Kentish plover, it has been found that males perform more anti-predator attacks than females during the brood-tending period (Brunton 1990; Fraga & Amat 1996; Hegyi & Sasvári 1998). There are differences between populations of Kentish plovers and even between years within a population in the timing of brood desertion by adults which are related to stochastic factors such as predation pressure (Amat *et al*. 1999). These factors modify the needs of chicks for biparental care, which explains why the timing of offspring desertion is not fixed. The results of our experiment on the effects of incubation duration on the timing of brood desertion indeed indicate that it is the needs of chicks for parental care rather than cumulative investment by females that dictates the timing of brood desertion in this sex.

In conclusion, brood desertion by female Kentish plovers cannot be explained by the differential parental capacity hypothesis in energetic terms as proposed by Erckmann (1983). Brood desertion is better explained by behavioural differences between the sexes in their capacity to provide parental care.

Financial support for this study was obtained from the Dirección General de Investigación Científica y Técnica (grants PB92-0115 and PB95-0110) and Plan Andaluz de Investigación (research group RNM 0105) of the Junta de Andalucía. The Consejería de Medio Ambiente, Junta de Andalucía, authorized our work at Fuente de Piedra, where Manuel Rendón, director of the nature reserve, provided many facilities. Berthe Verstappen and Trea Dijkstra skilfully performed the isotope analyses. Christophe Barbraud, Adrian H. Farmer, Brett K. Sandercok and Támas Székely commented on previous drafts of the manuscript.

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