

Why do Both Parents Incubate in the Kentish Plover?

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Abstract

Incubation by both parents is a common parental behaviour in many avian species. Biparental incubation is expected if the survival prospects of offspring are greatly raised by shared care, relative to the costs incurred by each parent. We investigated this proposition in the Kentish plover *Charadrius alexandrinus*, in which both parents incubate the clutch, but one parent (either the male or the female) usually deserts after hatching of the eggs. We carried out a mate-removal and food supplementation experiment to reveal both the role of the sexes and food abundance in maintaining biparental incubation by removing either the male or the female from the nest for a short period of time. In some nests we provided supplementary food for the parent that remained at the nest to reduce the costs of incubation, whereas other nests were left unsupplemented. Although males spent more time on incubation after their mate had been removed, females' incubation did not change. Notwithstanding the increased male incubation, total nest attentiveness was lower at uniparental nests than at biparental controls. However, incubation behaviour was not influenced by food supplementation. We conclude that offspring desertion during incubation is apparently costly in the Kentish plover, and this cost cannot be ameliorated with supplementary food.

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Introduction

Should a parent abandon its family in order to seek out a new mate? Such behaviour is common throughout the animal kingdom and it also occurs among birds, which are usually thought of as typifying monogamy and joint parenthood

by the male and the female. On the one hand, staying with the mate and helping it to raise the young may increase the youngsters' survival until adulthood, and thus care may enhance the reproductive success of parents. On the other hand, deserting the family and initiating a nest with a new mate may also boost the reproductive success of the parent, and in addition it reduces the cost of time and energy spent on raising the offspring. Therefore, sexual conflict over care exists between the sexes as to which (if either) should desert the offspring (Maynard Smith 1977; Grafen & Sibly 1978). Recent empirical and theoretical studies have shown that the solution of sexual conflicts, and thus the trade-off between caring and deserting decisions, is influenced by the gains from caring and deserting (Balshine-Earn 1997; Osorno 1999; Pilastro et al. 2001; reviewed by Székely et al. 1996), and by the process by which desertion decisions are reached (Houston & McNamara 1999). Furthermore, one parent may strategically manipulate its own state to 'force' its mate to provide care (Barta et al. 2002).

Biparental care and limited sexual conflict over desertion are expected if an unassisted parent is unable to raise the young until they are fully independent, the deserting parent has no chance to remate and reneest, or desertion does not increase the survival of the deserting parent. We investigated the first proposition in a small precocial shorebird, the Kentish plover *Charadrius alexandrinus* (body mass: about 41 g). In Kentish plover both parents incubate the clutch (Fraga & Amat 1996; Kosztolányi & Székely 2002) although shortly after hatching, either the female or the male may desert the brood (Lessells 1984; Amat et al. 1999; Székely & Cuthill 1999). The deserting parent trades off the gain from desertion (i.e. remating in a given breeding season) against the survival of the deserted brood (Székely & Williams 1995; Székely & Cuthill 2000). On the one hand, deserting the offspring at an early age is advantageous, as the gain from desertion, in terms of finding a new mate and reproducing, decreases over the season due to the seasonal decline in both mating opportunity and brood survival (Székely & Cuthill 1999; Székely et al. 1999). On the other hand, deserting too early can be costly: if the deserted parent is unable to raise the young on its own, this reduces the gain from the deserted brood to zero. The latter issue is the main focus of our current study.

We carried out a removal and a food supplementation experiment to test the short-term effects of uniparental care on incubation behaviour and body weight in the Kentish plover. A major reason why a parent is unable to cope with uniparental care is the foraging time that is required to replenish energy reserves (Erckmann 1983; Oring 1986). Therefore, we also investigated whether incubation behaviour and body mass of a single parent can be influenced by food supplementation. We predicted that if a parent is removed from the nest during incubation, the experimentally 'deserted' mate will not be able to compensate fully for the absence of its mate in terms of incubation time, and it will also lose body mass. We also predicted that the effect of mate removal can be attenuated by food supplementation; i.e. the reduction in incubation time and body mass will be smaller in supplemented, than in unsupplemented, parents.

Methods

Experimental Manipulation

We carried out the experiment at Lake Tuzla, southern Turkey (36°42'N 35°03'E), where Kentish plovers breed in the saltmarsh around the lake (Székely & Cuthill 1999). The breeding population was about 1000 pairs. The study was carried out in an area of approx. 52 ha on the north side of the lake.

Kentish plovers nest on the ground and their eggs are deposited into a shallow scrape. The duration of incubation (from laying the last egg until all eggs hatch) is 24.2 ± 0.2 (SE) d ($n = 139$ nests, A. Kosztolányi & T. Székely, unpubl. data). We investigated clutches of three eggs (modal clutch size). The nests were allocated randomly to five experimental groups: (i) female-only care, (ii) female-only care + food supplementation, (iii) male-only care, (iv) male-only care + food supplementation, and (v) control biparental nests. The experiment was carried out in blocks of five nests to control for seasonal effects. We investigated 65 nests in total.

The experiment lasted for 4 d at each nest. On day 1 both parents were caught on their nest and banded with a metal ring and an individual combination of colour rings. Their body mass was measured to the nearest 0.1 g. On day 2 the behaviour of parents at their nest was observed for 3 h. On day 3 both parents were recaptured and re-measured. Then at control nests both parents were released, whereas at the rest one parent was taken to captivity. A small (about 5 cm diameter) feeding tray was positioned approx. 25 cm from each nest, and at the supplemented nests mealworms (*Tenebrio molitor* larvae) were provided. On day 4 further mealworms were provided at supplemented nests and the behaviour of parent(s) was recorded for 3 h at each nest. Once the observation was completed on day 4, we recaptured the parents and measured their body mass. Finally, the removed parent was released from captivity. At supplemented nests 4×40 mealworms were provided in total: the first portion was given after capture of both parents on day 3, and the last was given at least 30 min before the beginning of observation on day 4. To control for the effect of nest visits the empty trays at unsupplemented nests were checked four times. The utilizable energy content of provided food was about 145 kJ in total (Merkle & Barclay 1996), whereas the field metabolic rate of Kentish plovers during incubation is about 103 kJ/d (Amat et al. 2000). Kentish plovers are insectivorous (Cramp & Simmons 1983), and they readily ate mealworms both in the field and in captivity. Observations verified that both males and females took mealworms at the nest: $69.2 \pm 6.2\%$ and $78.7 \pm 4.7\%$ of mealworms were eaten at female-only supplemented nests and male-only supplemented nests, respectively (t-test, $t_{24} = 1.23$, $p = 0.23$). However, it is not known what proportion of the mealworms was consumed by the targeted plovers.

The behaviour of parent(s) was recorded from a hide at about 45–70 m from the nest every 20 s for 3 h starting between 07:00 and 18:00 h (local time, i.e. GMT + 3 h). The samples started 15 min after the observer (AK) arrived at the observation point. There is a strong diel pattern in incubation behaviour

(Kosztolányi & Székely 2002), therefore the timing of behavioural records was matched on days 2 and 4 (± 1 h) for each nest.

The experiment was carried out in 2 yr: between 1 May and 20 Jun. in 1998 (30 nests) and between 15 Apr. and 20 Jun. in 1999 (35 nests). Incubation behaviour was not different between years (t-test on the change in total incubation time, see definition below: $t_{63} = 0.56$, $p = 0.58$). In 1998 we used a slightly different procedure at 15 nests, whereby the experiment lasted for 5 d at each nest (days 1–2: observations for 2 h on each day; day 3: manipulation; days 4–5: observations for 2 h on each day). Thus removal and food supplementation lasted for 2 d, and 5×30 mealworms were provided at each supplemented nest. We found no difference between the two protocols, as neither the change in total incubation time (t-test: $t_{28} = 1.064$, $p = 0.30$), nor the change in body mass (see definition below) was different between the protocols (t-tests: males: $t_{10} = 1.036$, $p = 0.33$; females: $t_6 = 1.72$, $p = 0.14$).

Clutches did not differ among the five treatment groups before manipulation with respect to laying date (i.e. the number of days between 1 Jan. and clutch completion), incubation stage (i.e. the number of days between clutch completion and day 1) and clutch volume (one-way ANOVAS: laying date: range 105–164 d, $F_{4,60} = 0.017$, $p = 0.99$; incubation stage: range 2–17 d, $F_{4,60} = 0.90$, $p = 0.47$; clutch volume: range: 20.8–27.4 cm³, $F_{4,60} = 1.29$, $p = 0.29$).

Ethical Note

The experiment involved temporary removal of the male or female of incubating pairs, so there are several ethical issues to consider. We note that the removal lasted on average only 1.6 d (range 0.9–2.3), so the intervention was of short duration. The birds were caught with funnel traps at their nest. The removed birds were kept in an aviary at the field site. The aviary consisted of five 2.5 m (W) \times 2.5 m (L) \times 0.8 m (H) purpose-built cages. A maximum of five plovers were housed in a cage at the same time. Ad libitum food and water were provided twice daily. Plovers were fed with Haith's Prosecto (a mix for insectivorous birds), live mealworms, boiled rice, chopped pieces of hard-boiled hens' eggs and eggshells. Two to four multi-vitamin droplets were added to their water every day. Fifty-two birds were removed altogether. Parents were released 100–200 m from their nest in good condition. We did not aim to monitor nests closely after release as a result of time constraints, although we noted that most birds returned to their mate and resumed incubation. In a previous removal experiment where detailed behavioural time budgets (including aggression) were collected, we detected no difference between the behaviour of released birds and that of the non-removed ones that stayed in the natural habitat (Székely & Cuthill 1999).

Our experiment was designed to induce a cost to the 'abandoned' parent: we predicted that in unsupplemented nests, the remaining parent would compensate for the shortfall in incubation by its mate, at the expense of lost energy reserves (but see Results as to whether this actually occurred). Permanent removal of the partner would have been desirable to measure the fitness costs of uniparental

incubation in terms of abandoned clutches, unhatched eggs and impaired chick growth or survival. However, we were interested in the short-term behavioural responses of parents and not in the effect of these changes on survival prospects of eggs and chicks.

Hatching success is naturally low in Kentish plover due to high rates of nest predation. In the current study at least 19 of 65 experimental pairs hatched their eggs, and this is not different from the hatching success of unmanipulated nests (at least 17 of 66 nests hatched, $\chi^2_1 = 0.20$, $p = 0.66$). Thus, our experimental design and the choice of sample size was a compromise between minimizing the costs imposed on the remaining parent whilst still being able to detect an effect of the experimental treatment. The experiment was licensed by Turkish Ministry for Natural Parks in a location where the Kentish plover is locally very abundant (Magnin & Yazar 1997).

Statistical Procedures

We considered each nest as the unit of analysis. Three behavioural variables were calculated both before and after manipulation for each nest: (i) total incubation was the percentage of time when the clutch was incubated by either parent, (ii) male incubation was the percentage of time when the nest was incubated by the male, and (iii) female incubation was the percentage of time when the nest was incubated by the female. We analysed both the post-manipulation behavioural variables, and the change in behaviour during the experiment, i.e. after manipulation–before manipulation. The change in body mass was calculated in a similar fashion. If several behavioural records or body mass measurements were available for a nest or a parent, we took their mean.

We made specific predictions about the results before the experiment was carried out, and thus used specific contrasts, i.e. planned comparisons, in the analyses (see Rosenthal et al. 2000). In the analyses of total incubation, four contrasts were used. First, the control nests were contrasted against all other nests; i.e. for the treatments (i)–(v) specified earlier, the contrast weights are 1, 1, 1, 1 and -4 (see Norusis 1988). Secondly, the effect of removal was investigated by comparing female-only and male-only nests with control ones (1, 0, 1, 0 and -2). Thirdly, the effect of food supplementation was investigated by comparing female-only and male-only nests with female-only + food and male-only + food (-1 , 1, -1 , 1 and 0). Fourthly, we looked for the effect of interaction between removal and food supplementation by contrast weights 1, -1 , -1 , 1 and 0, i.e. comparing female-only and male-only + food groups with female-only + food and male-only groups. If there was an interaction between the two treatments, then the latter contrast should be significant. We adopted a conservative approach in multiple comparisons and accepted $p = 0.0127$ as a critical level of significance that keeps the overall α at 0.05 when four comparisons are made ($1-0.95^{(1/4)}$; Motulsky 1995).

In the analyses of male incubation, female incubation and body mass, two sets of contrasts were used. First, the effect of removal was investigated by

comparing male-only or female-only nests to control ones ($-1, 0$ and 1 ; where the contrasts are given for single-parent, single-parent + food and control nests). Secondly, the effect of supplementation was investigated by comparing male-only nests to male-only + food, or female-only nests to female-only + food ($-1, 1$ and 0). In uniparental analyses we took $p = 0.0253$ as critical significance level. We give the results of contrast analyses (t values) in the text, and for completeness we also provide the result of one-way ANOVAS in figure legends.

Body mass of incubating female plovers change significantly during the day (Szentirmai et al. 2001). However, diurnal changes in body mass of parents are unlikely to confound our results, because the timing of captures before and after manipulation did not differ among the experimental groups (one-way ANOVAS, before manipulation: males: $F_{4,60} = 0.29$, $p = 0.88$; females: $F_{4,60} = 0.30$, $p = 0.88$; after manipulation: males: $F_{2,26} = 1.10$, $p = 0.35$; females: $F_{2,15} = 3.16$, $p = 0.072$).

Eleven nests were not attended during the post-manipulation observations, i.e. the eggs were not incubated by either parent, although the parents returned to some of these nests after the trial was completed. Therefore, we analysed the behavioural data in two ways: all nests were included in the analyses ('all nests' henceforward) or only those nests were included that were attended during the behavioural sample ('attended nests' henceforward). We inspected the distribution of residuals by quantile–quantile plots for skewness and kurtosis, and the distributions were approximately normal. We note that one-way ANOVAS and t -tests are robust to minor deviations from a normal distribution (Zar 1996; Quinn & Keough 2002), and conventional tests of normality such as Kolmogorov–Smirnov test have low statistical power due to small sample sizes. We used SPSS for Windows 8.0 in statistical analyses. $\bar{x} \pm SE$ and two-tailed probabilities are given.

Results

Uniparental nests were incubated for a lower percentage of time ($46.9 \pm 4.5\%$, $n = 52$) than biparental controls ($69.1 \pm 8.2\%$, $n = 13$; Fig. 1A, post-manipulation: $t_{60} = 2.18$, $p = 0.033$; change: $t_{60} = 2.55$, $p = 0.013$). The same trend is apparent when only the attended nests were considered (Fig. 1B, uniparental nests: $58.1 \pm 4.0\%$, $n = 42$; control: $74.8 \pm 6.3\%$, $n = 12$; post-manipulation: $t_{49} = 1.93$, $p = 0.059$; change: $t_{49} = 1.92$, $p = 0.061$). There was no interaction between removal and food supplementation (all nests, post-manipulation: $t_{60} = 0.62$, $p = 0.54$; change: $t_{60} = 0.39$, $p = 0.70$; attended nests, post-manipulation: $t_{49} = 0.091$, $p = 0.93$; change: $t_{49} = 0.23$, $p = 0.82$), so we now consider the main effects.

Effect of Removal

Female-only and male-only nests were incubated for a lower percentage of time than controls when only the attended nests were considered (Fig. 1B,

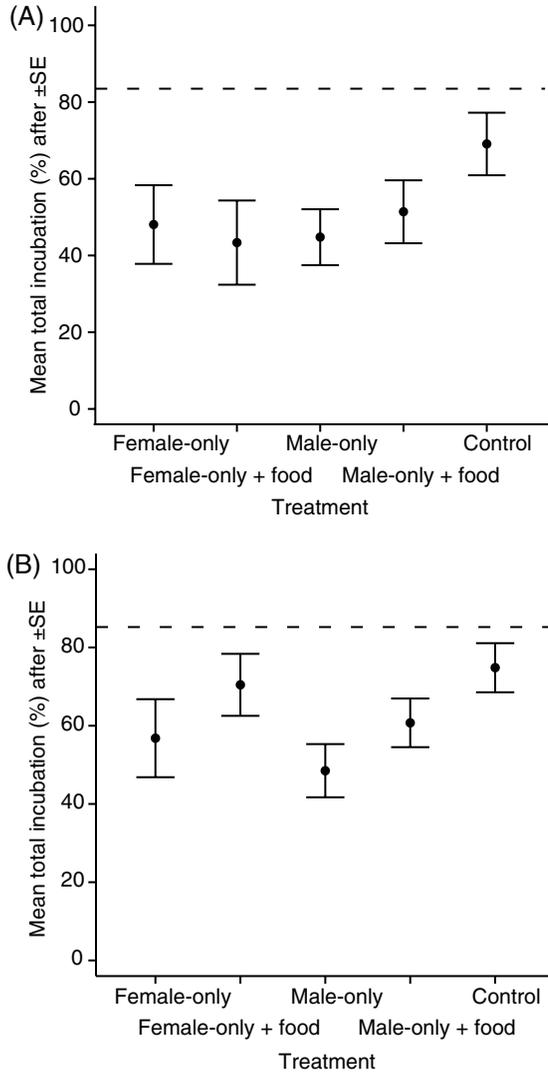


Fig. 1: Total incubation ($\bar{x} \pm SE\%$) after manipulation for (A) all nests and (B) attended nests only. Broken line indicates the mean of all nests before manipulation (one-way ANOVAS: all nests, post-manipulation: $F_{4,60} = 1.31$, $p = 0.28$; change: $F_{4,60} = 1.68$, $p = 0.17$; attended nests only, post-manipulation: $F_{4,49} = 2.057$, $p = 0.10$; change: $F_{4,49} = 1.68$, $p = 0.17$)

post-manipulation: $t_{49} = 2.51$, $p = 0.015$; change: $t_{49} = 2.24$, $p = 0.030$). This result is also apparent when all nests were considered (Fig. 1A, post-manipulation: $t_{60} = 2.036$, $p = 0.046$; change: $t_{60} = 2.35$, $p = 0.022$).

Males spent more time on incubation after their mate had been removed (Fig. 2, all nests, post-manipulation: $t_{36} = 2.91$, $p = 0.006$; change: $t_{36} = 3.59$,

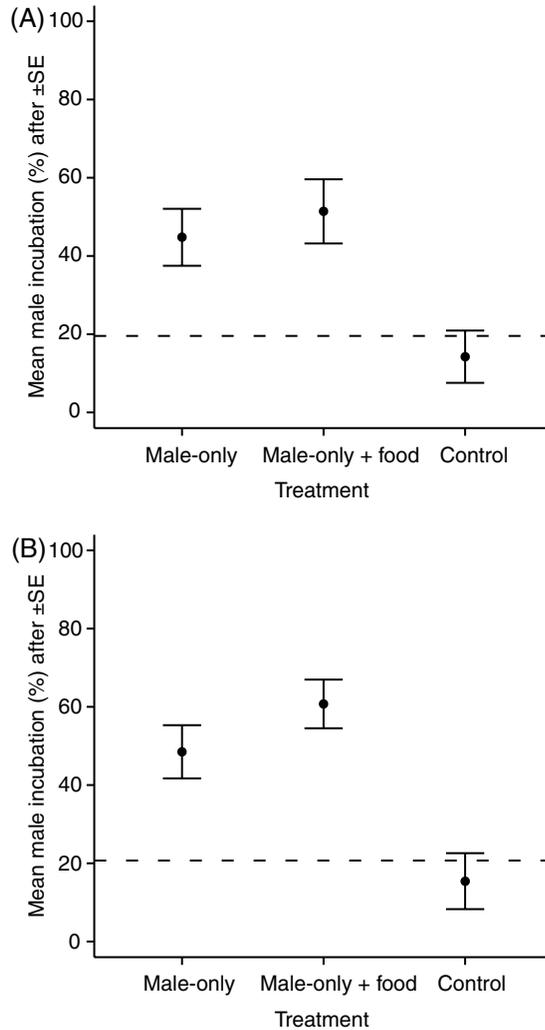


Fig. 2: Male incubation ($\bar{x} \pm \text{SE}\%$) after manipulation for (A) all nests and (B) attended nests only. Broken line indicates the mean of nests in the three groups before manipulation (one-way ANOVAS: all nests, post-manipulation: $F_{2,36} = 7.14$, $p = 0.002$; change: $F_{2,36} = 8.52$, $p = 0.001$; attended nests only, post-manipulation: $F_{2,32} = 11.97$, $p < 0.001$; change: $F_{2,32} = 8.54$, $p = 0.001$)

$p = 0.001$; attended nests, post-manipulation: $t_{32} = 3.50$, $p = 0.001$; change: $t_{32} = 3.50$, $p = 0.001$), whereas females' incubation did not change after the removal of their mate (Fig. 3, all nests, post-manipulation: $t_{36} = 0.46$, $p = 0.65$; change: $t_{36} = 1.46$, $p = 0.15$; attended nests, post-manipulation: $t_{28} = 0.21$, $p = 0.84$; change: $t_{28} = 0.95$, $p = 0.35$). Taken together, before manipulation females spent more time incubating the nest during daytime ($65.9 \pm 3.5\%$) than

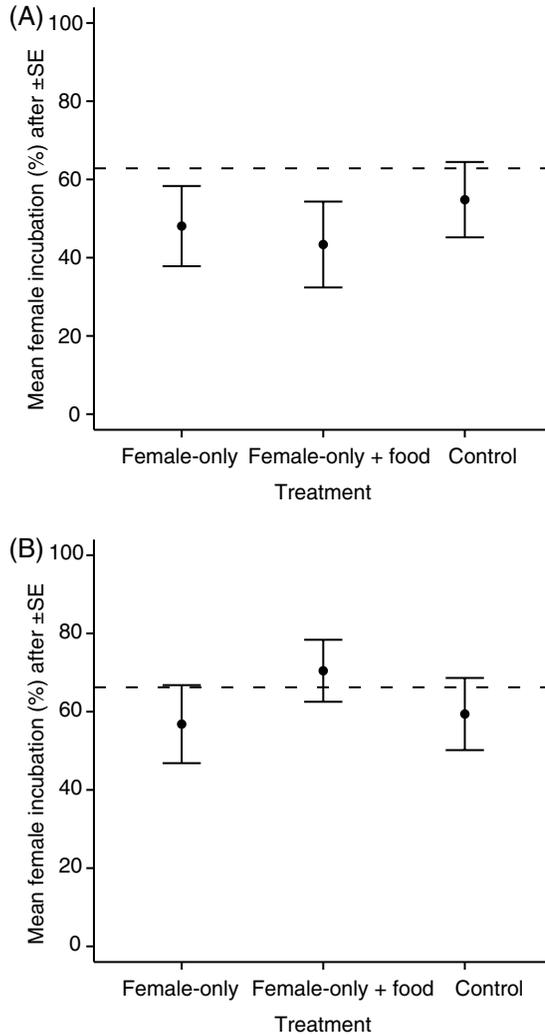


Fig. 3: Female incubation ($\bar{x} \pm \text{SE}\%$) after manipulation for (A) all nests and (B) attended nests only (one-way ANOVAS: all nests, post-manipulation: $F_{2,36} = 0.31$, $p = 0.73$; change: $F_{2,36} = 1.35$, $p = 0.27$; attended nests only, post-manipulation: $F_{2,28} = 0.51$, $p = 0.61$; change: $F_{2,28} = 0.51$, $p = 0.61$, see Fig. 2 for legend)

males ($17.5 \pm 3.2\%$; paired t -test: $t_{64} = 7.42$, $p < 0.001$), whereas after manipulation there was no difference between the sexes (t -tests, all nests: $t_{24} = 0.26$, $p = 0.80$; attended nests: $t_{21} = 0.70$, $p = 0.49$).

Males tended to lose mass after their mate had been removed (Fig. 4A, post-manipulation: $t_{26} = 3.48$, $p = 0.002$; change: $t_{26} = 1.41$, $p = 0.17$), whereas the body mass of females was not influenced by the removal of the male (Fig. 4B, post-manipulation: $t_{15} = 0.13$, $p = 0.90$; change: $t_{15} = 0.79$, $p = 0.44$).

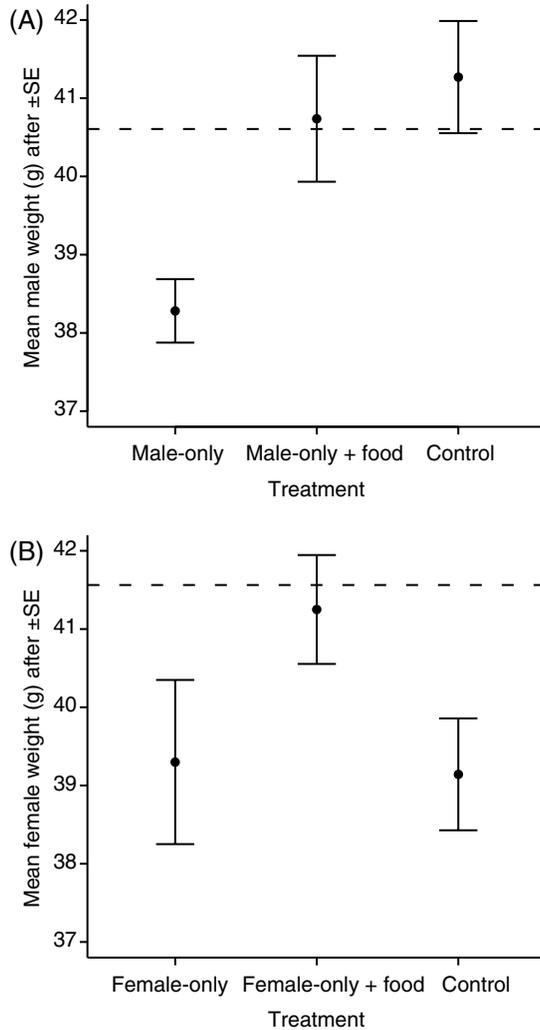


Fig. 4: Body mass ($\bar{x} \pm$ SE) after manipulation of (A) males and (B) females. Broken line indicates the mean body mass of a given sex before manipulation (one-way ANOVAS: male, post-manipulation: $F_{2,26} = 6.84$, $p = 0.004$; change: $F_{2,26} = 4.079$, $p = 0.029$; female, post-manipulation: $F_{2,15} = 1.32$, $p = 0.30$; change: $F_{2,15} = 0.41$, $p = 0.67$)

Effect of Food Supplementation

Food supplementation did not influence total incubation (Fig. 1, all nests, post-manipulation: $t_{60} = 0.11$, $p = 0.92$; change: $t_{60} = 0.047$, $p = 0.96$; attended nests, post-manipulation: $t_{49} = 1.67$, $p = 0.10$; change: $t_{49} = 1.075$, $p = 0.29$). Similarly, incubation behaviour was not influenced by the supplementation either in males (Fig. 2, all nests, post-manipulation: $t_{36} = 0.63$, $p = 0.53$; change:

$t_{36} = 0.022$, $p = 0.98$; attended nests, post-manipulation: $t_{32} = 1.27$, $p = 0.21$; change: $t_{32} = 0.21$, $p = 0.83$) or in females (Fig. 3, all nests, post-manipulation: $t_{36} = 0.32$, $p = 0.75$; change: $t_{36} = 0.076$, $p = 0.94$; attended nests, post-manipulation: $t_{28} = 0.97$, $p = 0.34$; change: $t_{28} = 0.74$, $p = 0.47$).

The body mass of supplemented males was significantly higher than the body mass of unsupplemented ones (Fig. 4A, post-manipulation: $t_{26} = 2.69$, $p = 0.012$; change: $t_{26} = 2.85$, $p = 0.008$), whereas we found no difference in females (Fig. 4B, post-manipulation: $t_{15} = 1.41$, $p = 0.18$; change: $t_{15} = 0.73$, $p = 0.48$).

Discussion

Our experiment showed that total incubation time decreased after the removal of one parent. Although males, which normally incubate mostly at night (Fraga & Amat 1996; Kosztolányi & Székely 2002), increased their time spent on incubation, this increase was not sufficient to replace the lost contribution of their mate. Females, which carry out nearly all incubation during daytime, did not change the time they spent on incubation. Unassisted females may have spent some time at night incubating the nest, and thus overall, the females may also have increased their incubation time over the full day. As a consequence of decreased total incubation, in nests incubated by only a single parent the embryonic development may slow down. Experimental results of Lessells (1983) in the Kentish plover showed that at uniparental nests the eggs were left unattended for a greater proportion of time than at biparental nests, and the incubation period was longer at unassisted nests than at biparental ones.

However, C. M. Lessells (pers. comm.) also found that unassisted plovers were capable of incubating up to 13 d (males) or 9 d (females) after the removal of their mate. If a single parent is capable of incubating for so long, why does uniparental desertion normally occur only after the chicks hatch? We suggest two costs of deserting the offspring before hatching. First, there is a risk that the deserted parent will terminate care and thus doom the clutch to failure. For instance, in our experiment 10 of 52 unassisted parents did not incubate during the behavioural sample, whereas in Lessells' study eight of 29 unassisted parents (two males and six females) deserted their nest. Secondly, in unassisted nests hatching time increases due to lower incubation constancy and thus the risk increases that the nest will be predated before it hatches (Webb 1987). In addition, the viability of eggs may decrease in unassisted nests, although Lessells found 100% hatching success of 15 eggs that survived this long. These possible costs suggest that deserting the clutch and mate may be a more costly behaviour in the Kentish plover than deserting the chicks. However, our study was not designed to detect long-term costs. For instance parents may need longer re-nesting period after experimentally raised parental effort, as has been shown in black swans (Brugger & Taborsky 1994).

However, the demand for biparental care is not the only reason for the occurrence of biparental care, because the parents may also stay with their mate and offspring if the pay-off from desertion is low (reviewed by Clutton-Brock

1991; Székely et al. 1996; Ligon 1999; Bennett & Owens 2002) or if their mate prevents them from attracting additional mates (Slagsvold & Lifjeld 1994). For instance, if remating opportunities are low, then parents may stay with their mate and help him/her to incubate (Székely et al. 2000). Experimental studies in semi-natural situations and observations in the field are consistent with this prediction, because male cichlids desert when they have high mating opportunities (Keenleyside 1983; Balshine-Earn & Earn 1998), and female rock sparrows *Petronia petronia* desert their brood when unmated males are available in the population (Pilastro et al. 2001). Nevertheless, experimental verification of such relationships in the field would be highly informative.

Food supplementation experiments are often carried out to investigate whether changes in body mass of breeding birds is an indicator of stress or a strategic decision to reduce flight cost (Hillström 1995; Slagsvold & Johansen 1998; reviewed by Cuthill & Houston 1997). The only study that has investigated parental behaviour in this context found, similarly to us, that incubation behaviour was not influenced by the supplementation in Lesser snow geese *Chen caerulescens* and Ross's geese *C. rossii* (Gloutney et al. 1999). There may be three reasons for this. First, both in our study and in Gloutney et al.'s study (1999) the food was provided in trays at nests, thus it is possible that not only the targeted birds consumed it, as it was indeed observed in some cases during the behavioural sample. Nonetheless, the significant change in body mass found in both studies suggests that some (or most) of these food items were taken by the targeted parents. Alternatively, the significant difference in body weight between supplemented and unsupplemented males may not reflect a difference in body condition, but a difference in gut content (Lessells, pers. comm.): unsupplemented males were not able to feed while sitting on the nest, whereas supplemented ones were provided with food at the nest. Thus future studies are warranted to explore how the time spent on incubating and feeding relate to body condition and gut contents of parents. Secondly, the supplemented diet was not sufficiently diverse to provide the full range of dietary requirements. This explanation agrees with the conclusion of Slagsvold & Johansen (1998) that only one of five supplementation experiments that used mealworms found an effect on body mass of females, whereas the only study that used natural food items (caterpillars) did find an effect (Cucco & Malacarne 1997). Thirdly, energetic requirement may not be the main driving force behind incubation schedules. For instance, male birds can take recesses in order to defend their territories. Separation of these mutually non-exclusive explanations requires further experiments.

In conclusion, our experiment suggests that the conflict over offspring desertion during incubation may be minimal in the Kentish plover, as the cost of uniparental desertion is apparently high. If either parent deserts the nest, then the number of hatchlings is expected to decrease, even if the deserted parent decides to stay and continue incubation. There still may be conflicts over the amount of care provided and such conflicts may drive the daily pattern of incubation. Future studies are needed to investigate how males and females solve this conflict and settle the level of parental effort observed during incubation.

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