

Tamás Székely · Tony D. Williams

Costs and benefits of brood desertion in female kentish plovers, *Charadrius alexandrinus*

Received: 5 March 1994/Accepted after revision: 14 May 1995

Abstract Female kentish plovers *Charadrius alexandrinus* typically desert their broods after the chicks hatch, i.e. 1–4 weeks before the chicks fledge or become independent. In this paper we investigate the costs and benefits of desertion for females. Desertion incurs a cost for females: following desertion chick survival in broods is lower ($0.95 \pm 0.02 \text{ day}^{-1}$) than before the female deserts ($0.98 \pm 0.01 \text{ day}^{-1}$). We investigated several possible causes for reduced brood survival by comparing characteristics of broods before and after desertion (controlling for differences in brood age). After desertion males increased the time they spent foraging and they tended to reduce time spent brooding chicks. Increased mortality of chicks may occur in deserted broods because following desertion (1) males spend less time alert in vigilance behaviour than before desertion, (2) they attend the chicks from greater distances, and (3) they show greater distraction display distances (in response to human intruders). Growth or development of chicks, measured by weight gain and tarsus length, was not different before and after desertion. Females gain two potential benefits from desertion: (1) they may remate and produce a second brood within the same breeding season or (2) they may enhance their probability of surviving to breed in a subsequent season. At least 27% of female kentish plovers that deserted remated and renested in the same season in this study. In contrast, we found no evidence that brood desertion increased the survival of females: there was no difference in local survival rate (return rate) for females deserting before or after 6 days brood age.

These results clearly demonstrate that female kentish plovers that desert their offspring prior to fledging incur costs, but we suggest that there is a trade-off with the potential benefits gained by remating and making a second breeding attempt in the same season.

Key words Female desertion · Parental care · Trade-off · Kentish plover · *Charadrius alexandrinus*

Introduction

The trade-off between current and future reproductive investment represents an important concept in life-history theory (Lessells 1991; Stearns 1992). In many seasonally breeding vertebrates this trade-off occurs on a relatively long time scale, for example between breeding attempts in successive years. However, such a trade-off can also be important over much shorter periods, and an example of this occurs with brood desertion (Clutton-Brock 1991; Davies 1991; T. Székely, J.N. Webb, A.I. Houston and J.M. McNamara unpublished work). Desertion has been defined as termination of care, by either one or both parents, before the offspring are capable of surviving independently (Fujioka 1989). This phenomenon has been reported in a variety of taxa including invertebrates, fish, amphibia, birds and mammals (Kleiman 1977; Blumer 1979; Forester 1979; Perrone and Zaret 1979; Wells 1981; Beissinger 1987; Ueda 1987; Nafus and Schreiner 1988; Diesel 1989; Kelly and Kennedy 1993). Desertion by either parent is particularly common in precocial birds such as in ratites, ducks and shorebirds (Lenington 1984; Bustnes and Erikstad 1991; Clutton-Brock 1991; Pöysä 1992).

Desertion involves a trade-off between the costs and/or benefits of continued investment in parental care in the current breeding attempt and those related to the bird's future fecundity or survival. Any explanation of desertion behaviour is therefore unlikely

T. Székely · T. D. Williams
Department of Animal and Plant Sciences,
Sheffield University, P.O. Box 601, Sheffield S10 2UQ, UK

T. Székely (✉)
Behavioural Ecology Research Group, Department of Zoology,
Kossuth University, Debrecen, H-4010, Hungary

T. D. Williams
Department of Biological Sciences, Simon Fraser University,
Burnaby, British Columbia, V5A 1S6, Canada

to be straightforward, because the deserting parent seemingly risks the survival of the current brood for potential future, and therefore unknown, benefits. Previous studies of birds have demonstrated that deserting individuals might benefit by being able to remate and initiate a second clutch shortly after desertion (Beissinger and Snyder 1987; Fujioka 1989; Persson and Öhrström 1989; Székely and Lessells 1993) or through earlier initiation of moult or migration (Myers 1981; Ezaki 1988; Urano 1992). In this situation, desertion behaviour will be adaptive if the second (deserted) parent is capable of raising the young to independence on its own such that the deserting bird incurs no (or little) cost of desertion in terms of decreased probability of survival of the first brood (Beissinger and Snyder 1987; Fujioka 1989). Even if the deserting bird leaves the brood before the other parent is completely able to compensate for the deserter's share of parental care, desertion will still be the better option for one of the parents than caring if the benefits of desertion exceed the costs (Maynard Smith 1977; Lazarus 1990; T. Székely, J.N. Webb, A.I. Houston and J.M. McNamara unpublished work). Numerous studies have investigated whether desertion behaviour is costly to deserting individuals in altricial species (Beissinger and Snyder 1987; Ezaki 1988; Fujioka 1989; Persson and Öhrström 1989). However, despite the prevalence of desertion behaviour there have been no similar studies on precocial birds in which desertion is part of the breeding strategy (Lenington 1984; Miller 1985; Warriner et al. 1986; Gratto-Trevor 1991).

In this study we investigate the costs and benefits of desertion in a precocial shorebird, the kentish plover, *Charadrius alexandrinus*. Specifically, we test the hypothesis that deserting females may incur costs because the deserted male is unable to compensate completely for the loss of care after the departure of the female. First, single males may be unable to spend as much time brooding chicks compared to two parents or they may initiate fewer brooding bouts (Lenington 1980). Second, single males may be less effective in protecting chicks from predators, e.g. they may spend less time in alert (vigilance) behaviour, they may attend chicks from further away, or they may take fewer risks in luring potential predators away from the chicks during distraction displays than in biparentally attended broods (Safriel 1975; Warriner et al. 1986; Larsen 1991). Third, single males may provide an inferior feeding territory for the brood, in which case chicks in deserted broods should show reduced growth rates compared to those in biparental broods (Walters 1982). We also test the hypothesis that desertion may be beneficial for female kentish plovers in two ways: (1) deserting females increase their reproductive success by remating and relaying subsequent to desertion (Székely and Lessells 1993) and (2) that deserting females increase their probability of over winter survival through early departure from the breeding site

and exploit of better feeding conditions at migratory stopover sites (Gratto-Trevor 1991).

Methods

Study sites and species

We investigated the costs and benefits of female desertion in a small (42 g) precocial shorebird, the kentish plover. This species has one of the most variable patterns of avian parental care: both parents incubate the clutch, but one parent frequently deserts the brood soon after hatching. The timing of desertion varies: some broods are deserted on the day of hatching, while others are attended by both parents until the chicks fledge (Lessells 1984; Székely and Lessells 1993; Székely and Williams 1994). Although desertion by either parent has been reported in both kentish plovers (Lessells 1984; Székely and Lessells 1993; P.E. Jönsson personal communication) and snowy plovers *C. a. nivosus* (Warriner et al. 1986), desertion by the female is more prevalent in all populations that have been studied to date.

Fieldwork was carried out in 1988–1994 at two sites, one in southern Hungary near the towns of Szeged and Kistelek, and one in central Hungary near the villages of Harta and Akasztó. In southern Hungary the study site comprised alkaline grasslands and fish-ponds, and in central Hungary one alkaline grassland ("Miklapusztá") was studied. The study sites and field methods are described fully elsewhere (Székely and Lessells 1993; Székely et al. 1994; Székely and Williams 1994).

Behavioral observations and capture of birds

We attempted to observe the behaviour of parents and chicks every other day, for 1 h in 1989–1991, and for 2 h in 1992. Observations were made from a hide or vehicle, usually at distances of 50–100 m from the brood. The behaviour of one parent was recorded at a time (for biparental broods we chose the bird closer to the centre of the brood, defined as "attending" parent) and behaviour was categorized as brooding, foraging, preening, standing, sitting, injury-feigning, running or flying. Parents attending broods typically adopted a characteristic upright standing posture or vigilance behaviour, and we therefore assumed that time spent standing corresponded to the time spent alert. We also recorded the total time when the parent was not visible either because it flew out of view or it was hidden by the vegetation. Only behavioural units lasting at least 5 s were recorded. For brooding bouts we recorded whether chick(s) or the attending parent initiated brooding. Chicks were considered to have initiated brooding when at least one chick ran to the parent. Parents initiated brooding either by moving toward the chick(s) or by lowering their breast, fluffing their breast feathers and calling the chicks. The distance between the attending parent and chick(s) was estimated visually every 10 min (all estimates made by T.S.). If either the parent or chick(s) were not visible, then the distance separating them when they first reappeared was used. When adults changed over brood attendance in biparental broods during an observation period, we continued to record the behaviour of the bird closest to the centre of the brood (the distinction between attending and off-duty parent was clear-cut in the majority of cases). We observed only two broods in which both parents simultaneously brooded the chicks (for 255 s and 45 s or 3.7% and 0.2% of total observation time for the two broods, respectively). Off-duty parents typically flew 0.5–1 km away from their broods. Behaviour of off-duty males in biparental broods was recorded either before or after the observations on the attending parent.

We attempted to capture broods at least every 4 days (in years 1988–1992). In 1991 and 1992 immediately after the chicks were caught the distraction display distance between the parent and

the observer (T.S.) was recorded every 10 s for 3 min, while the observer stood in the centre of the brood's previous location. We used this distance as a measure of intensity of anti-predator behaviour or brood defence (Brunton 1990). One parent was recorded at a time and in biparental broods we randomized whether the male or female was recorded first. If a parent flew out of view during the observation period, then the distance to the point of disappearance was recorded. We searched for females which had deserted their brood each day during the breeding season between 1988 and 1993. Five deserting females were identified with new mates before they laid the first egg of their second clutch and one female was identified after she laid a new clutch for her new mate. Females deserting broods between 1988 and 1993 were included in the analyses of local survival (return rates). Returning females were either observed on the study sites or were captured on their nests between 1989 and 1994; 17 deserting females were recaptured or resighted in the year subsequent to deserting their broods and four females were recaptured or resighted 2–3 years after they had deserted their broods.

Data handling and statistical analysis

If more than one set of behavioural observations were available for a single brood, we combined these records for each brood. For each combined record we calculated the net time during which the parent was visible, by subtracting the time spent both out of view and in cover from the total time of observation. The proportion of this net time that bird spent brooding, foraging, preening and in alert behaviour was then determined. Distances between parent and chick(s) were pooled for each family and a mean value calculated per brood. Hatching dates were known for most chicks and the ages of other chicks were estimated from the chicks' weight at the time of first capture (Székely and Lessells 1993). We attempted to locate broods every 2–4 days. The survival rate for each brood was then estimated using the Mayfield method (Mayfield 1975):

$$\text{Survival (in day}^{-1}\text{)} = 1 - \frac{\text{no. of chicks dying between two sightings}}{\text{initial no. of chicks} \times \text{no. of days between two sighting}} \quad (1)$$

This method has the assumption of instantaneous discovery of death, i.e. that death occurred in the 1-day interval before the second sighting. Survival rates were therefore estimated only when the resighting interval was ≤ 4 days (broods before desertion: 1.6 ± 0.1 days, $n = 17$; broods after desertion: 1.9 ± 0.2 days, $n = 17$).

Behaviour of the parent birds, and growth and survival of broods, may vary with age of the brood. To control for this effect, we took the combined data for each brood and fitted a linear regression, with brood age as the independent variable, for each analysis. All broods for which we had data either before or after the female deserted were included in the linear regressions. The residuals from these regression equations were then compared within broods where data were available both before and after female desertion. We used paired *t*-tests, or if the assumptions of normality or homogeneity of variances were not met then Wilcoxon matched-pairs tests, for these comparisons. By using each brood as its own control we were able to exclude confounding effects such as year of the study or location of the brood. Also, by controlling for brood age we took into account other variables such as brood size which may also covary over the age of the broods.

Remating rates and local survival (return rates) were calculated only for those deserting females which were ringed with unique combinations of colour rings. Deserting females were considered to have time to find new mates and lay second clutches if they deserted by 10 June. This was based on a clutch completion date for last clutches of 23 June (range 15 June–5 July between 1988 and 1993; T. Székely and G. Noszály unpublished work) assuming that deserting females took 2 days to remate (see Results) and 11 days to complete a clutch (Székely et al. 1994). Females were classified as “early”

or “late” deserters depending on whether they deserted their brood < 6 days or ≥ 6 days after hatching (mean desertion time was 5.9 days after hatching; Székely and Williams 1994). The time span between the last observation with the first brood and first observation once the female had deserted was 2.6 ± 0.5 days for females deserting < 6 days after hatching ($n = 19$ broods) and 7.8 ± 1.5 days for females deserting ≥ 6 days after hatching ($n = 17$ broods). These data included one brood for which the female was last seen with the fledged chicks 25 days after hatching. Only a single record was used for each female in the analyses of local survival rates. If a female deserted in more than 1 year then a single randomly selected brood was used. Estimates of local survival might be biased if the likelihood of females breeding but being undetected varied with timing of desertion. However, this is unlikely: 2 of 12 females and 2 of 9 females were not recorded in the year following desertion, for females deserting < 6 days and ≥ 6 days after hatching respectively, even though they were recorded 2–3 years after they deserted (Fisher's exact test, $P = 0.59$).

Statistical tests were carried out using SPSS for the Macintosh 4.0. Values are given as means \pm SE with two-tailed probabilities unless otherwise stated.

Results

Costs of desertion

Deserting females paid a cost in terms of decreased offspring survival in their original (deserted) brood. Before desertion chick survival was 0.983 ± 0.011 day $^{-1}$ compared to 0.950 ± 0.023 day $^{-1}$ after desertion. Using residuals from the linear regressions fitted to brood survival this difference was highly significant: before desertion: 0.05 ± 0.01 day $^{-1}$ versus after desertion: -0.03 ± 0.02 day $^{-1}$; Wilcoxon matched-pairs tests, $z = 2.58$, $P < 0.01$, $n = 17$ broods). The difference in chick survival was not related to differences in brood age as survival *increased* with the age of the brood (survival rate = $0.918 + 0.003 \times$ brood age (in day), $r = 0.341$, $P < 0.01$, $n = 56$ broods).

Before the desertion of broods by the female, the behaviour of the attending parents did not differ between sexes: males and females spent a similar proportion of their total time brooding, foraging, preening and in alert (vigilance) behaviour, and they initiated a similar proportion of total brooding bouts (Table 1; Wilcoxon matched-pairs test, $P > 0.58$ in all cases). In addition, there was no significant difference in the average distance at which male and female parents attended their broods (Table 1). After the female deserted the brood, the behaviour of the deserted male parent attending the brood changed significantly (Table 2). Males increased the time they spent foraging, from 8.6% to 47.2% ($P < 0.001$) and reduced the time they spent in alert or vigilance behaviour (Table 2). These changes in a deserted male's time budget may have reflected a requirement for increased feeding time. Before desertion males were probably able to meet their nutritional requirements by spending their off-duty time foraging; feeding was the most common activity of off-duty biparental males ($45.5 \pm 9.3\%$ of their off-duty

Table 1 Behaviour of parental kentish plovers attending broods before female desertion, and the distance between the attending parent and chick(s). Values are given as means \pm SE with sample sizes; only broods for which both parents were recorded in the same observation period were included

| | Male | Female | P^a | n |
|---|-----------------|----------------|-------|-----|
| Brooding (% time) | 52.6 \pm 9.0 | 49.5 \pm 7.7 | 1.00 | 16 |
| Alert (% time) | 24.4 \pm 6.3 | 26.5 \pm 6.0 | 0.61 | 16 |
| Foraging (% time) | 9.6 \pm 2.8 | 10.3 \pm 4.6 | 0.59 | 16 |
| Preening (% time) | 2.2 \pm 1.0 | 1.5 \pm 0.6 | 0.88 | 16 |
| Initiation of brooding (% by parent) ^b | 62.7 \pm 10.7 | 68.0 \pm 9.2 | 0.58 | 10 |
| Distance from chicks (m) | 7.2 \pm 5.8 | 1.7 \pm 0.6 | 0.36 | 17 |

^aProbabilities of Wilcoxon matched-pairs tests between males and females.

^bPercent initiation by attending parent as a proportion of total no. of initiations by attending parent and chick(s)

time was spent feeding, $n = 12$ males). This is significantly higher than the proportion of time spent feeding by males in biparentally-attended broods ($10.5 \pm 2.8\%$, $n = 19$ males, Mann-Whitney U -test, $z = 3.45$, $P < 0.001$).

There were also significant differences in the brood defence behaviour of males before and after female desertion. Males attended their chicks at a closer distance before desertion (1.4 ± 0.6 m) than after desertion (6.2 ± 1.3 m; paired t -test on residuals, $t = 2.60$, $P = 0.02$, $n = 13$ broods). Males also performed distraction displays, in response to the human observer, at a greater distance from the brood's location before desertion (62.5 ± 12.3 m) than after desertion (102.1 ± 8.0 m) although this difference was only marginally significant (paired t -test on residuals, $t = 2.46$, $P = 0.07$, $n = 5$ broods).

We found no indication that deserted males were less able to provide good quality feeding areas for their chicks following desertion, based on chick growth. Development of chicks measured as rate of weight

gain or increase in tarsus length were not significantly different before and after female desertion (Table 3).

Benefits of desertion

We recorded a minimum 27% of females that deserted before 10 June renesting with a second mate in the same season (6 females out of 22). However, there appeared to be marked annual variation in renesting rate. Between 1988 and 1991 none of nine deserting females were found renesting, whereas five of seven females in 1992 and one of six females in 1993 renested after desertion. Five deserting females were observed with their new mates 2.0 ± 0.6 days (range: 1–4 days) after they deserted their broods (all data from 1992). Five out of six clutches laid by deserting females failed during incubation, and the remaining female successfully hatched two chicks. We found no evidence for enhanced survival of females in relation to brood desertion: 12 out of 19 females deserting their brood < 6 days after hatching and 9 out of 18 deserting ≥ 6 days after hatching returned to the study sites in subsequent years (1–3 years after desertion; chi-square test, $\chi^2 = 0.66$, $P > 0.4$).

Discussion

Cost of desertion

In this study of the precocial kentish plover we found evidence that females that desert their broods prior to chick independence or fledging incur costs in terms of a decrease in the fitness of their current (deserted) brood. Although the difference in offspring survival between biparentally attended and deserted or uniparental broods appears unimpressive (only 3.3% day^{-1}), for females deserting their brood at hatching this would lead to an overall 38% difference in brood survival between hatching and fledging (at

Table 2 Behaviour of attending male parent before and after desertion by their mate in kentish plover. Values are given as means \pm SE, with residuals for the regression of behaviour (dependent variable) and brood age (independent variable) in parentheses; only broods recorded both before and after desertion of the female were included

| | Before desertion | | After desertion | | P^a | n |
|--|------------------|---------|-----------------|---------|-------|-----|
| Brooding (% time) | 56.7 \pm 9.5 | (13.3) | 16.8 \pm 6.0 | (3.2) | 0.3 | 13 |
| Alert (% time) | 21.8 \pm 6.7 | (5.0) | 22.6 \pm 5.7 | (-17.4) | 0.02 | 13 |
| Foraging (% time) | 8.6 \pm 3.1 | (-20.3) | 47.2 \pm 7.3 | (14.8) | 0.001 | 13 |
| Preening (% time) | 2.5 \pm 1.2 | (-0.5) | 4.7 \pm 1.8 | (-0.4) | 0.8 | 13 |
| Init. of brooding (% by male) ^b | 63.8 \pm 9.5 | (9.2) | 30.7 \pm 9.8 | (-22.3) | 0.2 | 7 |

^aBehaviour was compared before and after desertion by testing the residual behaviour from the linear regression fitted to brood age (independent variable), using Wilcoxon matched-pairs test.

^bPercent initiation by attending parent as a proportion of total no. of initiations by attending parent and chick(s)

Table 3 Growth rates of chicks before and after desertion by the female parent in kentish plover. Values are means \pm SE, with residuals for the regression of weight or size (dependent variable) and brood age (independent variable) in parentheses; only broods captured both before and after desertion of the female were included

| | Before desertion | | After desertion | | P^a | n |
|------------------------|------------------|---------|-----------------|--------|-------|-----|
| Weight change (g/day) | 0.68 \pm 0.09 | (-0.01) | 1.10 \pm 0.04 | (0.06) | 0.3 | 14 |
| Tarsus growth (mm/day) | 0.33 \pm 0.05 | (-0.02) | 0.42 \pm 0.06 | (0.07) | 0.2 | 14 |

^aGrowth rates were compared before and after desertion by testing the residual change in weight or tarsus length calculated from the linear regression fitted to brood age (independent variable), using paired t -tests

28.0 \pm 0.9 days of age; T. Székely unpublished work). One possible explanation for the lower survival rates of chicks in deserted broods might be that these broods are "low-quality", due to characteristics of the chicks themselves or the male parent, that these broods tend to be deserted more often or sooner after hatching than "high-quality" broods, and that the chicks in these broods have an inherently lower probability of survival. We consider this explanation unlikely for several reasons. Firstly, in our analysis we compared within the same brood before and after desertion, and this should have controlled for potential confounding factors such as quality of mate or brood. Secondly, there is no difference in the behaviour, size or body condition of male parents for broods which were deserted early or late by their mates (Székely and Williams 1994).

Previous studies have failed to find a cost of desertion in terms of brood survival between deserted and biparental broods, e.g. in little egret *Egretta garzetta* (Fujioka 1989), snail kite *Rostrhamus sociabilis* (Beissinger 1987; Beissinger and Snyder 1987) and great reed warbler *Acrocephalus arundinaceus* (Ezaki 1988). In these three species desertion occurs when the chicks are near to independence, in contrast to the situation in the kentish plover where females typically desert the broods well before the chicks reach independence. Our data further suggest that in the kentish plovers the cost of female desertion is related to the inability of the male parent to fully compensate for the loss of parental care arising from the departure of the female. It appears most likely that the time-budget of deserted male kentish plovers was constrained by the demands for self-feeding, which normally would be met during the off-duty period when the bird's partner attends the brood. Lenington (1980) found in killdeer *Charadrius vociferus* that off-duty parents spent about 40% of their total time feeding, and this time is similar to the proportion of time spent feeding in deserted and off-duty male kentish plovers. When males share parental care with their mates they can feed when they are away from their broods, but deserted males must fit all their activities around more or less constant brood attendance.

We found support in this study for the hypothesis that biparentally-attended broods enjoyed better protection from predators, compared to deserted uniparental broods (*sensu* Safriel 1975; Warriner et al.

1986). Time spent by males in the alert or vigilance-posture was significantly higher before desertion than after, and males of biparentally-attended broods took greater risks by approaching a potential predator more closely during distraction displays, than did deserted males. Further studies are required to test other potential predation-related advantages of biparental care such as earlier detection or aggressive deterrence of predators (Larsen 1991).

There was no evidence in kentish plover that chicks attended by both parents gained access to superior feeding areas: there was no significant difference in growth of chicks before and after desertion. This advantage of biparental care may be more relevant in dense populations, where good feeding sites are limited and the parents have to protect their chicks from the attacks of neighbouring adults (Warriner et al. 1986). Kentish plovers breed at low density (0.2–1.2 nests/ha, Székely 1992) in inland sites, compared with coastal populations where densities range from 5–16 nests/ha in southern Portugal (T. Székely unpublished work) to 143 pairs/ha in Germany (Rittinghaus 1961). Consistent with this hypothesis, single-parents of deserted broods spend 4–5% of their time in aggressive interactions in high density populations, whereas they spend < 1% of time fighting at low density (T. Székely unpublished work).

Benefits of desertion

If deserting females incur a cost of desertion, we would predict that this should be "balanced" by a benefit of desertion (Maynard Smith 1977; Lazarus 1990). Based on the results of this study we suggest that this primary benefit that female kentish plover obtain by deserting their current brood is an increased probability of remating and producing a second clutch in the same season. At least 27% of deserting female kentish plovers remated and re-nested shortly after desertion. In the snowy plover remating is also common and the frequency of re-nesting is even higher than we recorded for kentish plover: at least 37% of snowy plover females deserting their broods re-nest with new mates in the same season (Warriner et al. 1986). Remating was also very rapid in kentish plovers with females pairing with new

mates within 1–4 days after desertion. This may be explained by the male biased sex ratio shown both in kentish plover and snowy plover (P.E. Jönsson personal communication; Warriner et al. 1986). Furthermore, other studies have shown that birds may disperse following desertion remating and completing their second breeding attempt at considerable distances from their original breeding site. For example, snail kites may move distances up to 160 km between successive breeding attempts (Beissinger and Snyder 1987), and between successive matings a single female penduline tit (*Remiz pendulinus*) and snowy plover were recorded moving 200 km and 220 km, respectively (Franz et al. 1987; G.W. Page personal communication). If such post-desertion dispersal occurs in kentish plover this strongly suggests that our estimate of 27% reneesting underestimates the true reneesting rate, and therefore underestimates the potential benefits of female desertion.

A further benefit that females may gain by deserting their current brood is enhanced survival and increased probability of returning to breed in subsequent seasons (Myers 1981; Ezaki 1988; Urano 1992). We found no support for this hypothesis in kentish plover although we predict that this advantage may be particularly important in Arctic-nesting, rather than temperate-zone, shorebirds. Female semipalmated sandpipers *Calidris pusilla* have a relative energy deficit by the end of the incubation period (Ashkenazie and Safriel 1979). By terminating parental care shortly after hatching the female of this species may be able to leave the breeding grounds and reach the migratory stopover sites earlier, taking advantage of better feeding conditions at these more southerly sites (Gratto-Trevor 1991). Nevertheless, Gratto-Trevor (1991) also failed to find any differences in survival between females deserting their broods and those remaining with their broods to fledging. Desertion might also enhance female survival if continued parental care had mortality costs. For example, there are reports of incubating and brood-attending shorebirds having been killed by predators when protecting their broods, in semipalmated sandpiper and killdeer (Brunton 1986; Gratto-Trevor 1991).

In conclusion, this study has demonstrated that desertion of broods prior to chicks becoming independent is costly to females in terms of decreased survival of the female's current brood. This appears to occur because deserted males are unable to fully compensate for the loss of parental care arising from the departure of their mates. Foraging time may constrain the time-budget of deserted males. Females trade-off this cost of desertion by capitalizing on the male-biased sex ratio and by rapidly remating and producing a second clutch following desertion.

Acknowledgements Field work for this project was supported by the Hungarian Ministry for Environment, The Association for the Study of Animal Behaviour and an OTKA grant to T.S. (no. T5492). Kiskunság National Park provided the licence for the field

work including ringing. Hartai Állami Gazdaság provided logistic support for the study, for which we also thank G. Schneider, L. Fazekas and G. Krómer. We also acknowledge the assistance of M. Castro, J. Kis, S. Kovács, A. Liker and G. Noszály. T.S. was supported by an ASAB and Hungarian Postdoctoral Fellowship of The Royal Society during the preparation of the manuscript; T.D.W. was supported by a Royal Society University Research Fellowship. Drs. S. R. Beissinger, J. V. Briskie, C. L. Gratto-Trevor, B. Kempnaers, C. M. Lessells and J. D. Reynolds provided useful comments on earlier versions of this manuscript.

References

- Ashkenazie S, Safriel UN (1979) Time-energy budget of the semipalmated sandpiper *Calidris pusilla* at Barrow, Alaska. *Ecology* 60: 783–799
- Beissinger SR (1987) Mate desertion and reproductive effort in the snail kite. *Anim Behav* 35: 1504–1519
- Beissinger SR, Snyder NFR (1987) Mate desertion in the snail kite. *Anim Behav* 35: 477–487
- Blumer L (1979) Male parental care in bony fishes. *Q Rev Biol* 54: 149–161
- Brunton DH (1986) Fatal antipredator behavior of a killdeer. *Wilson Bull* 98: 605–607
- Brunton DH (1990) The effects of nesting stage, sex, and type of predator on parental defense by killdeer (*Charadrius vociferous*): testing models of avian parental defense. *Behav Ecol Sociobiol* 26: 181–190
- Bustnes JO, Erikstad KE (1991) Parental care in the common eider (*Somateria mollissima*): factors affecting abandonment and adoption of young. *Can J Zool* 69: 1538–1545
- Clutton-Brock TH (1991) The evolution of parental care. Princeton University Press, Princeton
- Davies NB (1991) Mating systems. In: Krebs JR, Davies NB (eds) *Behavioural ecology*. Blackwell, Oxford, pp 263–294
- Diesel R (1989) Parental care in an unusual environment: *Metopaulias depressus* (Decapoda: Grapsidae), a crab that lives in epiphytic bromeliads. *Anim Behav* 38: 561–575
- Ezaki Y (1988) Mate desertion by male great reed warblers *Acrocephalus arundinaceus* at the end of the breeding season. *Ibis* 130: 427–437
- Forester DC (1979) The adaptiveness of parental care in *Desmognathus ochrophaeus* (Urodela: Plethodontidae). *Copeia* 1979: 332–341
- Franz DN, Theiss N, Graff H (1987) Female of penduline tit (*Remiz pendulinus*) breeding successfully twice in one breeding-season at two places in a distance of more than 200 km. *J Ornithol* 128: 241–242
- Fujioka M (1989) Mate and nestling desertion in colonial little egrets. *Auk* 106: 292–302
- Gratto-Trevor CL (1991) Parental care in semipalmated sandpipers *Calidris pusilla*: brood desertion by females. *Ibis* 133: 394–399
- Kelly EJ, Kennedy PL (1993) A dynamic state variable model of mate desertion in Cooper's hawks. *Ecology* 74: 351–366
- Kleiman DG (1977) Monogamy in mammals. *Q Rev Biol* 52: 39–69
- Larsen T (1991) Anti-predator behaviour and mating systems in waders: aggressive nest defence selects for monogamy. *Anim Behav* 41: 1057–1062
- Lazarus J (1990) The logic of mate desertion. *Anim Behav* 39: 672–684
- Lenington S (1980) Bi-parental care in killdeer: an adaptive hypothesis. *Wilson Bull* 92: 8–20
- Lenington S (1984) The evolution of polyandry in shorebirds. In: Burger J, Olla BL (eds) *Shorebirds. Breeding behavior and populations*. Plenum, New York, pp 149–167
- Lessells CM (1984) The mating system of kentish plovers *Charadrius alexandrinus*. *Ibis* 126: 474–483

- Lessells CM (1991) The evolution of life histories. In: Krebs JR, Davies NB (eds) Behavioural ecology. Blackwell, Oxford, pp 32–68
- Mayfield HF (1975) Suggestions for calculating nest success. *Wilson Bull* 87:456–466
- Maynard Smith J (1977) Parental investment: a prospective analysis. *Anim Behav* 25:1–9
- Miller EH (1985) Parental behavior in the least sandpiper (*Calidris minutilla*). *Can J Zool* 63:1593–1601
- Myers JP (1981) Cross-seasonal interactions in the evolution of sandpiper social systems. *Behav Ecol Sociobiol* 8:195–202
- Nafus DM, Schreiner IH (1988) Parental care in a tropical nymphalid butterfly *Hypolimnas anomala*. *Anim Behav* 36:1425–1431
- Perrone M, Zaret TM (1979) Parental care patterns of fishes. *Am Nat* 113:351–361
- Persson O, Öhrström P (1989) A new avian mating system: ambisexual polygamy in the penduline tit *Remiz pendulinus*. *Ornis Scand* 20:105–111
- Pöysä H (1992) Variation in parental care of common golden eye (*Bucephala clangula*) females. *Behaviour* 123:247–260
- Rittinghaus H (1961) *Der Seeregenpfeifer*. Ziemsen, Wittenberg Lutherstadt
- Safriel UN (1975) On the significance of clutch size in nidifugous birds. *Ecology* 56:703–708
- Stearns SC (1992) The evolution of life histories. Oxford University Press, Oxford
- Székely T (1992) Reproduction of kentish plover *Charadrius alexandrinus* in grasslands and fish-ponds: the habitat mal-assessment hypothesis. *Aquila* 99:59–68
- Székely T, Lessells CM (1993) Mate change by kentish plovers *Charadrius alexandrinus*. *Ornis Scand* 24:317–322
- Székely T, Williams TD (1994) Factors affecting timing of brood desertion by female kentish plovers *Charadrius alexandrinus*. *Behaviour* 130:17–28
- Székely T, Karsai I, Williams TD (1994) Determination of clutch-size in the kentish plover *Charadrius alexandrinus*. *Ibis* 136:341–348
- Ueda K. (1987) Brood desertion in the fan-tailed warbler *Cisticola juncidis*. *Jap J Ornith* 36:13–18
- Urano E (1992) Early settling the following spring: a long-term benefit of mate desertion by male great reed warblers *Acrocephalus arundinaceus*. *Ibis* 134:83–86
- Walters JR (1982) Parental behavior in lapwings (Charadriidae) and its relationships with clutch sizes and mating systems. *Evolution* 36:1030–1040
- Warriner JS, Warriner JC, Page GW, Stenzel LE (1986) Mating system and reproductive success of a small population of polygamous snowy plovers. *Wilson Bull* 98:15–37
- Wells KD (1981) Parental behavior of male and female frogs. In: Alexander RD, Tinkle DW (eds) Natural selection and social behavior. Chiron, New York, pp 184–197

Communicated by R. Montgomerie