Trade-off between mating opportunities and parental care: brood desertion by female Kentish plovers

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Why do some parents care for their young whereas others divorce from their mate and abandon their offspring? This decision is governed by the trade-off between the value of the current breeding event and future breeding prospects. In the precocial Kentish plover *Charadrius alexandrinus* females frequently, but not always, abandon their broods to be cared for by their mate, and seek new breeding partners within the same season. We have shown previously that females' remating opportunities decline with date in the season, so brood desertion should be particularly favourable for early breeding females. However, the benefits are tempered by the fact that single-parent families have lower survival expectancies than those where the female remains to help the male care for the young. We therefore tested the prediction that increasing the value of the current brood (by brood-size manipulation) should increase the duration of female care early in the season, but that in late breeders, with reduced remating opportunities, desertion and thus the duration of female care should be independent of current brood size. These predictions were fulfilled, indicating that seasonally modulated trade-offs between current brood value and remating opportunities can be important in the desertion decisions of species with flexible patterns of parental care.

Keywords: offspring desertion; parental care; mating opportunity; brood size; *Charadrius alexandrinus*

1. INTRODUCTION

Brood desertion is a behavioural trait that occurs in many animals including insects, fishes, amphibians, birds and mammals (reviewed by Clutton-Brock 1991; Sargent & Gross 1993; Crump 1996; Székely *et al.* 1996). By deserting the offspring the parents trade-off the pay-off from continuing care against the pay-off from terminating care. On the one hand, if the parents continue care, then they may boost the ability of their young to survive until adulthood. On the other hand, if the parents terminate care they may gain two sorts of benefits: (i) they may increase their reproductive success by initiating a new brood shortly after desertion (e.g. Balshine-Earn 1995; Beissinger 1990; Verhulst *et al.* 1997), or (ii) they may improve their own survival or breeding success in future breeding seasons (e.g. Urano 1992; Eens & Pinxten 1995; Osorno 1999).

The trade-off between the pay-offs from caring and deserting is influenced by various ecological, behavioural and life-history variables (reviewed by Clutton-Brock 1991; Székely *et al.* 1996) including the number and viability of offspring, and the probability of finding a new mate. It is important to understand this trade-off, since it lies at the heart of many mating and parental care decisions, and thus it has implications for the evolution of mating and caring patterns (Reynolds 1996; Székely *et al.* 2000). The most appropriate way to investigate this trade-off is in those species in which brood desertion naturally occurs (Clutton-Brock 1991). We investigate one such species, the Kentish plover *Charadrius alexandrinus*, a precocial shorebird (body mass is *ca.* 42 g) with a modal clutch size of three eggs (Székely *et al.* 1999). Both parents incubate the clutch, although one parent, typically the female, deserts the brood (Warriner *et al.* 1986; Székely &

Williams 1995; Amat *et al.* 1999). Thus some broods are raised by both parents, whereas in others only one parent, typically the male, cares for the brood until the chicks fledge.

Previous studies suggest that a within-season trade-off between caring and deserting occurs in the Kentish plover. First, females increase their reproductive success by staying with and caring for their brood (Székely & Williams 1995; Székely & Cuthill 1999), because they help their mate to defend the broods against predators and conspecifics that may kill their chicks (Amat *et al.* 1999; Székely *et al.* 1999). The pay-off from caring, however, decreases over the breeding season, since broods hatched late in the season have a lower survival probability than broods hatched early (Székely & Cuthill 1999). Second, females may also increase their reproductive success by deserting their brood, since deserting females often remate and renest. For example, at least 37% and 27% of deserting females renested with a new mate in California and Hungary, respectively (Warriner *et al.* 1986; Székely & Williams 1995). Remating time of females increases over the breeding season (Székely *et al.* 1999), and thus females deserting broods that hatched late in the season have a diminishing chance of remating and raising another brood, which may produce only a few, if any, young. Therefore, the trade-off between caring for the current brood and remating in the given breeding season should occur in early broods, but not in late ones.

The objective of our study was to investigate the trade-off between the value of current brood and remating by manipulating the brood size. We predicted that early in the breeding season small broods should be deserted at a younger age than large broods. In contrast, late in the season we did not expect such an effect, since the deserting female would have no chance of remating and completing a breeding attempt successfully before the season ends.

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The influence of brood size on parental care has frequently been studied in altricial birds, where provisioning rate often increases with brood size, at the expense of further breeding opportunities within the same season, or survival and reproduction in future seasons. However, the influence of current brood size on parental investment in precocial species, where care does not involve direct feeding, has received less attention.

2. METHODS

(a) *Experimental manipulation*

The experiment was carried out in Tuzla Lake, southern Turkey (36°42'N, 35°03'E), where Kentish plovers breed in the saltmarsh around the lake (Székely & Cuthill 1999; Székely *et al.* 1999). The breeding population was about 1000 pairs. We investigated three sites on the north side of the lake, referred to as sites A (107 ha), B (32 ha) and C (19 ha). Site A was nearest to Tuzla village and site C the farthest.

Experimental manipulations were carried out between 6 May and 17 June 1998. All broods ($n = 48$) were biparental at the time of manipulation. A randomized block design was used to control for seasonal variation in desertion behaviour and brood survival. On any one date (block) groups of six nests were randomly allocated to the treatments: reduced to one chick (R1, $n = 8$ broods), reduced to two chicks (R2, $n = 8$ broods), control ($n = 16$ broods), enlarged to four chicks (E4, $n = 8$ broods) and enlarged to five chicks (E5, $n = 8$ broods). These manipulations are within the natural range, since brood size varies between one and seven chicks in unmanipulated broods (T. Székely, unpublished observations), although three is by far the most common brood size at hatching. Two types of controls were used: the chicks were either not manipulated ($n = 10$ broods), or one chick each was swapped between two broods ($n = 6$ broods). We did not detect any difference between the two types of control (Mann–Whitney U -tests, brood survival, $U = 26.5$, $p = 0.713$; duration of female care in broods that survived until over 25 days, $U = 16.0$, $p = 1.000$), and thus they were combined in the analyses (C3 broods). Eighteen chicks were removed from reduced broods and added to enlarged ones. In addition, five chicks were removed from reduced broods and added to broods not in the experiment, and seven chicks were added to enlarged broods from broods that were not in the experiment. The allocation of the latter chicks to non-experimental broods was necessary because, at the time of manipulation of these broods, there was no available brood of appropriate size and age that could donate or adopt the chicks. The added chicks were readily accepted by their new parents. The experiment was licensed by the Turkish Ministry for Natural Parks in a location where Kentish plovers are abundant (Székely & Cuthill 1999). The frequency of reduced (R1, R2), control (C3) and enlarged broods (E4, E5) was not different between study sites (log-likelihood ratio test, $G = 3.241$, d.f. = 4, $p = 0.518$).

In all broods both parents and their chicks were caught, ringed and measured. Each parent was ringed with a unique combination of colour rings. Forty-six broods hatched three chicks each and had three chicks when brood-size manipulation took place, whereas in two broods two chicks hatched from three eggs. In the latter broods the third chick failed to hatch after either one chick had been removed, or two chicks had been added, and thus these broods were included in the study as an R1 and an E4 brood, respectively.

Nests were checked at least daily near the expected date of hatching. Thirty-eight broods were manipulated either after the chicks started to peep in the eggs, or zero to two days after the chicks hatched. The chicks in all 38 broods were either in the nest-scape, or they were ringed on the day of hatching and recaptured for the manipulation one to two days later. The hatching date of ten broods was not known and the ages of these broods were estimated as zero to five days (see Székely & Cuthill (1999) for details). Brood age and body mass of chicks at the time of manipulation, and their hatching date (i.e. the number of days since 1 March) were not different between treatments (Kruskal–Wallis tests, brood age, $\chi^2 = 6.444$, $p = 0.168$; hatching date; $\chi^2 = 2.811$, $p = 0.590$; body mass, one-way ANOVA, $F_{4,43} = 1.19$, $p = 0.330$).

Brood checks, resightings of adults and captures of chicks were carried out as described by Székely & Cuthill (1999). Brood checking intervals did not differ between treatments (R1, 2.5 ± 0.2 (s.e.) days; R2: 2.5 ± 0.2 days; C3, 2.7 ± 0.2 days; E4, 3.0 ± 0.5 days; E5, 3.2 ± 0.3 days; one-way ANOVA, $F_{4,43} = 1.187$, $p = 0.330$).

An electric fence was installed in site C and in part of site B on 13 May to protect nests from mammalian predators (mainly golden jackals *Canis aureus* and stray dogs *Canis familiaris*). The chicks and adult Kentish plovers were able to move freely between the fenced and unfenced areas. The fence was removed on 23 June. There was no difference between treatment groups in the proportion of time they spent inside and outside the fence (Kruskal–Wallis test, $\chi^2 = 1.657$, $p = 0.799$).

(b) *Statistical procedures*

Each brood was considered as the unit of analysis. Desertion by the female was identified if either the female was observed with a new mate, or if she was not seen to attend her brood in at least two consecutive records. We considered two records of absence sufficient, because they correctly identified the occurrence of desertion in 18 out of 20 broods in which only the male attended the brood in at least three consecutive records. Duration of female care was the difference between hatching date and the date of female desertion, taken as the midpoint between the last date when both parents were observed with their brood and the first date when the female did not attend. Duration of female care was calculated only for those broods ($n = 38$ broods) in which either the female deserted, or at least one chick survived until the age of 25 days and the female stayed with her brood until 25 days. Kentish plover chicks fledge at *ca.* 28 days (Székely & Cuthill 1999). Duration of female care differed between sites: site A (24.7 ± 0.4 days, $n = 10$), B (13.5 ± 2.2 days, $n = 17$) and C (16.3 ± 2.8 days, $n = 11$, Kruskal–Wallis test, $\chi^2 = 11.427$, $p = 0.003$); thus we calculated the residual female care by taking the difference between duration of female care in a particular brood and the average for that site. Broods were divided into early (i.e. hatched before 30 May) and late (hatched on or after 30 May) to split the data on desertion behaviour as equally as possible. This date was also suitable since in a previous experiment (Székely *et al.* 1999) we found that unmated female Kentish plovers that were released from temporary captivity before 30 May typically found a new mate (13 out of 16 females), whereas unmated females released after 30 May rarely remated (two out of 11 females, Fisher's exact test, $p = 0.002$). Egg volumes were not different between females released early (8.06 ± 0.12 cm³, $n = 16$) and late (8.23 ± 0.10 cm³, $n = 11$, $t = 1.06$, $p = 0.299$), indicating little difference in the overall quality of these females.

Figure 1. Duration of care by female Kentish plovers (residual number of days) in relation to hatching date (number of days since 1 March, $b = 0.331$, $n = 38$, $p = 0.001$). These data do not include biparental broods that perished before 25 days. Overlapping data (2) are indicated by enlarged dots.

Female care was also investigated using survival regression (MINITAB 1997, v.12), and in these analyses we refer to the response variable as 'expected female care'. In the survival regression all observations were used for all broods and desertion by the female was the terminal event. An exponential distribution was used, since it provided the best fit to the observations. Non-significant interaction terms (between treatment and site) were removed from the models.

Survival of each brood was estimated by the maximum-likelihood method (see details in Noszály *et al.* 1995; Székely *et al.* 1999). This gives a value between zero (all chicks die within one to three days of manipulation) and 1.00 (all chicks survive until 25 days). Three chicks in two E5 broods were excluded from the analyses of brood survival, because two of these chicks were adopted by a neighbour pair, and one chick was killed during trapping three days after manipulation. The maximum-likelihood method was also used to calculate brood survival before a parent deserted the brood. The growth of young was investigated by analysing the slope of growth curves (see rationale in Székely *et al.* 1999). If several chicks of a brood were recaptured on a given date, we took the average of their measurements for that date.

Parametric tests were used if the assumptions of normality and heteroscedasticity of residuals were met. For least-squares linear regressions we provide F and b , the regression coefficient. The growth of chicks was analysed by ANCOVAs in which site was the factor and brood size was the covariate. In ANCOVAs we checked the interactions between factor and covariate; they were not significant. Mean $\pm$ s.e. are given unless otherwise indicated. All tests were two-tailed.

3. RESULTS

(a) Duration of female care

The female stayed with her brood for more than 25 days in 17 broods (eight early broods and nine late broods), whereas she deserted 11.0 ± 1.6 days (range 0.5–24 days) after hatching in 21 broods (early broods, 7.3 ± 1.7 days, $n = 12$; late broods, 15.9 ± 2.2 days, $n = 9$). In two C3 broods in which the female stayed with her brood the male deserted on 2.5 days and 20 days after hatching.

Figure 2. Duration of care by female Kentish plovers (residual number of days) in relation to brood size in broods (a) hatched early in the season ($b = 2.756$, $n = 20$, $p = 0.041$), and (b) hatched late in the season ($b = 0.058$, $n = 18$, $p = 0.956$). Overlapping data (one each) are indicated by enlarged dots.

In broods hatched late in the season the female stayed longer with her chicks than in early broods (figure 1; $F_{1,36} = 12.628$, $p = 0.001$). In early broods the residual female care increased with brood size (figure 2a; $F_{1,18} = 4.845$, $p = 0.041$), whereas in late broods the brood-size manipulation did not influence the residual female care (figure 2b; $F_{1,16} = 0.003$, $p = 0.956$). We also investigated whether residual female care was related to brood survival preceding female desertion. However, residual female care was unrelated to brood survival either in early broods (Spearman's rank correlations, $r_s = 0.232$, $n = 15$, $p = 0.203$), or in late ones ($r_s = 0.034$, $n = 18$, $p = 0.446$).

These analyses, however, did not take into account those broods in which all chicks died before 25 days and both parents still attended the chicks at the last observation. Thus we also used survival regression to investigate whether duration of female care related to brood size when taking into account such censored observations. These results confirmed the preceding analyses, since in broods hatched early in the season the expected female care increased with brood size (table 1; $z = 2.24$, $p = 0.025$), whereas in late broods the relationship remained non-significant between brood size and expected female care ($z = 0.46$, $p = 0.644$). Furthermore, brood survival preceding female desertion remained unrelated to expected female care both in early broods ($z = 0.87$, $p = 0.384$) and in late ones ($z = 0.30$, $p = 0.765$).

Table 1. Survival regression on the expected female care (dependent variable) in early ($n = 20$) and late ($n = 28$) broods of Kentish plover (covariate, brood size; factor, site)

(These analyses included biparental broods that perished before 25 days as censored observations.)

	regression coefficient	early broods		regression coefficient	late broods	
		z	p		z	p
intercept	3.466	2.93	0.003	4.299	4.28	0.000
brood size	0.509	2.24	0.025	0.112	0.46	0.644
site ^a	—	4.89	0.087	—	3.63	0.163

^a χ^2 and the probability of χ^2 are given, as d.f. = 2.

(b) Brood survival and growth

Few enlarged broods fledged all their young (one out of eight E4 broods and one out of six E5 broods; figure 3), whereas most reduced broods fledged all young (seven out of eight R1 and four out of eight R2). Causes of death of most chicks were unknown, although predators that were observed to attempt capturing chicks included golden jackals, stray dogs and spur-winged plovers *Vanellus spinosus*. The death of one chick is known; it was hit by a vehicle.

The manipulation influenced brood survival, since survival decreased with brood size ($r_s = -0.361$, $n = 48$, $p = 0.012$). Specifically, early in the season brood survival decreased with brood size (table 2; $r_s = -0.454$, $n = 20$, $p = 0.044$), and there was a non-significant trend in late broods ($r_s = -0.298$, $n = 28$, $p = 0.123$). Since brood survival increased with the distance from Tuzla village, i.e. from site A (0.819 ± 0.073 , $n = 17$), through B (0.962 ± 0.015 , $n = 20$) to C (0.986 ± 0.006 , $n = 11$, $r_s = 0.301$, $n = 48$, $p = 0.038$), we repeated the preceding analyses by controlling for the effect of site by partial Spearman's rank correlations (Daniel 1990). The partial rank correlations confirmed the preceding analyses in that once the effect of site was controlled for, then brood survival remained significantly related to brood size (partial rank correlations, $r_s = -0.349$, d.f. = 45, $p = 0.008$). This relationship remained significant in broods hatched early in the season ($r_s = -0.488$, d.f. = 17, $p = 0.017$), and there was a similar non-significant trend in late broods ($r_s = 0.252$, $n = 25$, $p = 0.102$).

The growth of chicks was not influenced by the brood-size manipulation (table 2). In particular, early in the season changes in neither body mass nor tarsus length were related to brood size (ANCOVAs: body mass, $F_{1,15} = 0.88$, $p = 0.364$; tarsus, $F_{1,14} = 1.60$, $p = 0.226$) and site (body mass, $F_{2,15} = 1.94$, $p = 0.179$; tarsus, $F_{2,14} = 2.08$, $p = 0.162$). Similarly, in late broods changes in neither body mass nor tarsus length were influenced by brood size (body mass, $F_{1,19} = 3.29$, $p = 0.086$; tarsus, $F_{1,19} = 1.27$, $p = 0.274$) and site (body mass, $F_{2,19} = 3.04$, $p = 0.071$; tarsus, $F_{2,19} = 3.43$, $p = 0.053$).

4. DISCUSSION

The results of our study are consistent with the explanation that female Kentish plovers trade off the benefit from their brood care against the benefit of deserting. As predicted, this trade-off occurred in early broods, but not in late ones.

Figure 3. Box plot of the number of young that survived until 25 days after hatching ($n = 8, 8, 16, 8, 6$ broods, from left to right; see § 2). The line is drawn across the median, the bottom and the top of the box are lower quartiles (Q_1) and upper quartiles (Q_3), respectively. The whiskers extend from the lower and the upper quartiles to the lowest and highest observation, respectively, within the range defined by $Q_1 - 1.5 \times (Q_3 - Q_1)$ and $Q_3 + 1.5 \times (Q_3 - Q_1)$. An outlier outside the upper or lower whiskers is plotted with an asterisk (MINITAB 1997).

Offspring desertion has been shown to relate to clutch size and brood size in various taxa (reviewed by Clutton-Brock 1991; Székely *et al.* 1996). For example, small clutches are more often deserted than large ones in fishes (Taborsky 1985; Wisenden 1994), birds (ten Cate & Taborsky 1992; Delehanty & Oring 1993; reviewed by Székely *et al.* 1996) and mammals (Tait 1980; Mendl 1994). Our results are also consistent with experimental manipulations of brood size in common goldeneye *Bucephala clangula* and snail kite *Rostrhamus sociabilis* where reduced broods were deserted more often than control ones (Beissinger 1990; Eadie & Lyon 1998). Our study, however, goes further by showing that the trade-off between brood size and subsequent reproduction specifically occurs early in the season when remating opportunities are still high.

Other studies, however, have found no relationship between brood size and desertion behaviour. For example, frequency of desertion did not differ between small and large broods in common goldeneye and great tit *Parus major* (Pöysä *et al.* 1997; Horak *et al.* 1999). Both latter studies argued that brood mortality is a better predictor of desertion than brood size, since broods with high mortality were more often deserted than broods with low mortality. These studies, however, were non-experimental and thus their results are open to alternative explanations. For example, young females (or the ones in poor body condition) might produce low quality broods that have poor survival, and these females may also have the tendency to desert their young (Székely *et al.* 1996). Although our study was not specifically designed to investigate the effects of offspring viability on desertion behaviour, the results do not support the relationship between brood mortality and desertion. Experimental manipulation of brood size as well as offspring quality is required to tease apart these effects on desertion behaviour.

Desertion may also confer other advantages than allowing further breeding attempts in a given breeding

Table 2. *Brood survival (median, interquartile range) and growth of chicks (mean ± s.e. change in body mass or tarsus length) in relation to brood size in broods hatched early in the season and in late ones (see § 2)*

	brood size					<i>r</i> _S (<i>n</i>) or <i>F</i> (d.f.,d.f.)	<i>p</i>
	1	2	3	4	5		
early broods							
survival	1.000, 0.0	1.000, 0.0	0.963, 0.039	0.967, 0.029	0.974, 0.048	− 0.454 (20) ^a	0.044
body mass (g d ^{−1})	0.529 ± 0.139	0.898 ± 0.013	0.753 ± 0.094	0.703 ± 0.156	0.722 ± 0.059	0.88 (1,15) ^b	0.364
tarsus (mm d ^{−1})	0.328 ± 0.080	0.395 ± 0.018	0.391 ± 0.037	0.355 ± 0.022	0.421 ± 0.057	1.60 (1,14) ^b	0.226
late broods							
survival	1.000, 0.138	1.000, 0.125	1.000, 0.095	0.671, 0.868	0.976, 0.141	− 0.298 (28) ^a	0.123
body mass (g d ^{−1})	0.736 ± 0.393	1.018 ± 0.115	0.745 ± 0.376	0.796 ± 0.067	0.572 ± 0.162	3.29 (1,19) ^b	0.086
tarsus (mm d ^{−1})	0.457 ± 0.140	0.508 ± 0.130	0.397 ± 0.131	0.409 ± 0.092	0.412 ± 0.091	1.27 (1,19) ^b	0.274

^a*r*_S and probability of Spearman's rank correlation are given (number of broods). ^b*F*-value (d.f._{factor}, d.f._{error}) and probability of covariant are given.

season. Parental care is often costly and thus the deserting parent(s) may reduce or eliminate such costs. For example, experimental manipulations of brood size have shown that parents raising enlarged broods suffer from higher mortality than females raising control broods (Daan *et al.* 1996; reviewed by Lessells 1991). Also, raising enlarged broods may have various fertility costs in the year following manipulation (reviewed by Dijkstra *et al.* 1990; Lessells 1991).

An alternative explanation for the long duration of female care in late broods may be that these broods could have a greater demand than early broods due to adverse conditions, i.e. the fitness increment from biparental care may be higher for late broods than for early ones. First, downy chicks are brooded for a substantial amount of time (> 50% of parents' time, Székely & Williams 1995), and thus an increased demand for brooding may be one such explanation. However, this explanation is unlikely, since the ambient temperature increases as the season progresses, so brooding time should decrease over the season. Second, the need to protect the young may increase over the season. For example, the frequency of predators or the number of competing Kentish plover families (and thus the opportunity for infanticide) may increase. The latter hypothesis requires further investigation, preferably by experimentally manipulating the breeding densities and quantifying the responses in fighting behaviour and brood desertion.

One may argue that seasonal variation in either brood value or in the cost of reproduction may confound our results. These arguments, however, are unlikely. First, although brood value (in terms of brood survival) does change over the breeding season in the Kentish plover (Székely & Cuthill 1999), this explanation would predict that females should provide better care for broods hatched early in the season (that have higher chances of surviving) than for late broods. Our results show the opposite pattern (figure 1). Second, the cost of raising young (in terms of surviving until future seasons and/or reproduction in future years) may increase over the season. For example, females attending broods hatched late in the season may have to moult later than females attending early broods. This explanation is also inconsistent with our results,

because the duration of female care was shorter in early broods than in late ones (figure 1).

Our experimental alterations of brood size have shown that brood survival decreased with brood size. This suggests that the parents were unable to compensate for the increased demand of care. This result might be expected in altricial birds, in which the parents feed their young (reviewed by Wolf *et al.* 1990; Dijkstra *et al.* 1990). However, in precocial birds, such as the Kentish plover, this result is surprising, since parental care is often considered 'non-depreciable', i.e. the benefits of care for the young do not decline with brood size (Clutton-Brock 1991). There are only three previous studies that experimentally investigated the effect of brood size on brood survival in precocial birds (Safriel 1975; Lessells 1986; Loonen *et al.* 1999). Brood survival was lower in enlarged broods than in controls in semipalmated sandpiper *Calidris pusilla* (Safriel 1975), whereas the other studies found no effect in Canada goose *Branta canadensis* and barnacle goose *Branta leucopsis* (Lessells 1986; Loonen *et al.* 1999). In shorebirds, such as Kentish plover and semipalmated sandpiper, most chicks that disappeared were probably taken by predators (Safriel 1975; this study) and/or were killed by conspecifics breeding in adjacent territories. The increased risk of predation and/or infanticide in large broods is plausible, since chicks are probably spread over a larger area and thus parental protection is less efficient. In geese, however, the dominance status of the family increases with brood size (Williams *et al.* 1994; Loonen *et al.* 1999), and thus chicks in enlarged broods have better access to feeding sites and grow faster (Loonen *et al.* 1999). Taken together, we suggest that a potential explanation for the different effects of brood size on brood survival between shorebirds (semi-palmated sandpiper and Kentish plover) and geese (Canada goose and barnacle goose) is the outcome of these two processes (i.e. cost in terms of increased vulnerability and benefit in terms of increased dominance).

In conclusion, our study suggests that female Kentish plovers trade off the value of their current young against the pay-off from deserting. This trade-off, however, occurs only in broods hatched early in the season. These results provide support for theoretical studies that suggest

the existence of such season-dependent trade-offs in parental care decisions (Webb *et al.* 1999).

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REFERENCES

- Amat, J. A., Fraga, R. M. & Arroyo, G. M. 1999 Brood desertion and polygamous breeding in the Kentish plover *Charadrius alexandrinus*. *Ibis* **141**, 596–607.
- Balshine-Earn, S. 1995 The costs of parental care in Galilee St Peter's fish, *Sarotherodon galilaeus*. *Anim. Behav.* **50**, 1–7.
- Beissinger, S. R. 1990 Experimental brood manipulations and the monoparental threshold in snail kites. *Am. Nat.* **136**, 20–38.
- Clutton-Brock, T. H. 1991 *The evolution of parental care*. Princeton University Press.
- Crump, M. L. 1996 Parental care among the Amphibia. In *Parental care: evolution, mechanisms, and adaptive significance* (ed. J. C. Rosenblatt & C. T. Snowdon), pp. 109–144. San Diego, CA: Academic Press.
- Daan, S., Deerenberg, C. & Dijkstra, C. 1996 Increased daily work precipitates natural death in the kestrel. *J. Anim. Ecol.* **65**, 539–544.
- Daniel, W. W. 1990 *Applied nonparametric statistics*. Boston, MA: PWS-KENT Publishing Company.
- Dehanty, D. J. & Oring, L. W. 1993 The effect of clutch size on incubation persistence in male Wilson's phalaropes, *Phalaropus tricolor*. *Auk* **110**, 521–528.
- Dijkstra, C., Bult, A., Bijlsma, S., Daan, S., Meijer, T. & Zijlstra, M. 1990 Brood-size manipulations in the kestrel *Falco tinnunculus*: effects on offspring and parent survival. *J. Anim. Ecol.* **59**, 269–286.
- Eadie, J. M. & Lyon, B. E. 1998 Cooperation, conflict, and creching behavior in goldeneye ducks. *Am. Nat.* **151**, 397–408.
- Eens, M. & Pinxten, R. 1995 Mate desertion by primary female European starlings at the end of the nestling stage. *J. Avian Biol.* **26**, 267–271.
- Horak, P., Jenni-Eiermann, S. & Ots, I. 1999 Do great tits (*Parus major*) starve to reproduce? *Oecologia (Berl.)* **119**, 293–299.
- Lessells, C. M. 1986 Brood size in Canada geese: a manipulation experiment. *J. Anim. Ecol.* **55**, 669–689.
- Lessells, C. M. 1991 The evolution of life histories. In *Behavioural ecology* (ed. J. R. Krebs & N. B. Davies), pp. 32–68. Oxford, UK: Blackwell.
- Loonen, M. J. J. E., Bruinzeel, L. W., Black, J. M. & Drent, R. H. 1999 The benefit of large broods in barnacle geese: a study using natural and experimental manipulations. *J. Anim. Ecol.* **68**, 753–768.
- Mendl, M. 1994 How should parents respond to a reduction in litter size: abandonment or extra care? *Behav. Process.* **31**, 285–291.
- MINITAB 1997 *User's guide, release 12*. State College, USA: MINITAB, Inc.
- Noszály, G., Székely, T. & Hutchinson, J. M. C. 1995 Brood survival of Kentish plovers (*Charadrius alexandrinus*) in alkaline grasslands and drained fish-ponds. *Ornis Hungarica* **5**, 15–21.
- Osorno, J.-L. 1999 Offspring desertion in the magnificent frigatebird: are males facing a trade-off between current and future reproduction? *J. Avian Biol.* **30**, 335–341.
- Pöysä, H., Virtanen, J. & Milonoff, M. 1997 Common goldeneyes adjust maternal effort in relation to prior brood success and not current brood size. *Behav. Ecol. Sociobiol.* **40**, 101–106.
- Reynolds, J. D. 1996 Animal breeding systems. *Trends Ecol. Evol.* **11**, 68–72.
- Safriel, U. N. 1975 On the significance of clutch size in nidifugous birds. *Ecology* **56**, 703–708.
- Sargent, R. C. & Gross, M. R. 1993 Williams' principle: an explanation of parental care in teleost fishes. In *Behaviour of teleost fishes* (ed. T. J. Pitcher), pp. 333–361. London: Chapman & Hall.
- Székely, T. & Cuthill, I. C. 1999 Brood desertion in Kentish plover: the value of parental care. *Behav. Ecol.* **10**, 191–197.
- Székely, T. & Williams, T. D. 1995 Costs and benefits of brood desertion in female Kentish plovers, *Charadrius alexandrinus*. *Behav. Ecol. Sociobiol.* **37**, 155–161.
- Székely, T., Webb, J. N., Houston, A. I. & McNamara, J. M. 1996 An evolutionary approach to offspring desertion in birds. In *Current ornithology*, vol. 13 (ed. V. Nolan Jr & E. D. Ketterson), pp. 271–330. New York: Plenum Press.
- Székely, T., Cuthill, I. C. & Kis, J. 1999 Brood desertion in Kentish plover: sex differences in remating opportunities. *Behav. Ecol.* **10**, 185–190.
- Székely, T., Webb, J. N. & Cuthill, I. C. 2000 Mating patterns, sexual selection and parental care: an integrative approach. In *Vertebrate mating systems* (ed. M. Apollonio, M. Festa-Bianchet & D. Mainardi), pp. 194–223. London: World Science Press.
- Taborsky, M. 1985 On optimal parental care. *Z. Tierpsychol.* **79**, 331–336.
- Tait, D. E. N. 1980 Abandonment as a reproductive tactic—the example of grizzly bears. *Am. Nat.* **115**, 800–808.
- ten Cate, C. & Taborsky, M. 1992 To raise or to abandon a reduced clutch: a theoretical approach illustrated using ringed turtle-doves (*Streptopelia risoria*). *Auk* **109**, 594–600.
- 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.
- Verhulst, S., Tinbergen, J. M. & Daan, S. 1997 Multiple breeding in the great tit. A trade-off between successive reproductive attempts? *Funct. Ecol.* **11**, 714–722.
- Warriner, J. S., Warriner, J. C., Page, G. W. & Stenzel, L. E. 1986 Mating system and reproductive success of a small population of polygamous snowy plovers. *Wilson Bull.* **98**, 15–37.
- Webb, J. N., Houston, A. I., McNamara, J. M. & Székely, T. 1999 Multiple patterns of parental care. *Anim. Behav.* **58**, 983–993.
- Williams, T. D., Loonen, M. J. J. E. & Cooke, F. 1994 Fitness consequences of parental behavior in relation to offspring number in a precocial species: the lesser snow goose. *Auk* **111**, 563–572.
- Wisenden, B. D. 1994 Factors affecting mate desertion by males in free-ranging convict cichlids (*Cichlasoma nigrofasciatum*). *Behav. Ecol.* **5**, 439–447.
- Wolf, L., Ketterson, E. D. & Nolan Jr, V. 1990 Behavioural response of female dark-eyed juncos to the experimental removal of their mates: implications for the evolution of male parental care. *Anim. Behav.* **39**, 125–134.