



**Costs and benefits of parental care in the
Kentish plover *Charadrius alexandrinus***

PhD thesis

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Thesis

Introduction

Parental care is one of the most variable behavioural traits of animals (Clutton-Brock 1991, Westneat & Sargent 1996). There are different forms of care (e.g. lactation in mammals or incubation in birds), and the length of care may also vary from a few days to several years. The number and sex of caring parent is also highly variable. In mammals usually only the female cares, whereas in fishes male-only care is common, and birds are typically biparental (Krebs & Davies 1993, Reynolds et al. 2002). Parental care is rare in invertebrates, but it does occur in various taxa, for instance in social insects. Variation of care exists not only between distantly related taxa, but also between populations or individuals (Westneat & Sargent 1996). This diversity of caring patterns is interrelated with the high variety of mating systems (Reynolds 1996, Székely et al. 2000).

The obvious benefit of care is the higher survival success of offspring. However, the time and energy invested in the current offspring may be traded off against the future reproductive expectations of the parent (cost of reproduction, Williams 1966, Roff 1992). This cost may not only result in decreased survival or future fecundity of the parent, but also in lost opportunity of remating in the same breeding season. Because of these costs, it would be beneficial for each parent to leave the task of caring to the other parent, and invest resources in its own survival and in its future reproductive attempts. Therefore, a conflict should exist between the parents over care (Trivers 1972, Parker et al. 2002). Arguably, this conflict over the length and amount of parental investment has led to the observed highly variable pattern of parental care across taxa (Balshine et al. 2002).

The degree of sexual conflict over care depends on the relative costs and benefits of care. Biparental care and limited conflict over care is expected if care by both parents increases the number of surviving offspring or if the opportunity for remating is low for both parents (Maynard Smith 1977, Lessells 1999). Furthermore, sexual conflict also depends on the extent of shared interests between the pair members in their current and future breeding attempts (Lessells 1999). For instance, extra-pair fertilisations reduce the paternity of the male, and thus the common interest in the current clutch, therefore intense conflict is expected. The extent of conflict is minimal in species in which the interests of males and females fully coincide in future (e.g. in case of lifetime monogamy). The solution of the conflict may often be the reduced effort of the parent, or even the desertion of offspring (Székely et al. 1996, Webb et al. 1999, McNamara et al. 2000).

To understand how males and females resolve the conflict over care, we need to know the type and shape of resource allocation trade-offs involved in different

aspects of reproduction. A large proportion of life-history studies that aimed to explore these trade-offs was conducted in birds. Birds generally breed more than once in their life-time, and their reproductive behaviour can be divided into four discrete phases: courtship and mating, egg laying, incubation and brood rearing. Therefore, birds are ideal to study the effects of different trade-offs both between the different phases of the same breeding attempt and between different reproductive attempts (Reid et al. 2002). Most studies, however, focused only on the brood-rearing phase, and considered the previous phases of reproduction as they play little or no role in cost of reproduction (but see Monaghan et al. 1998).

Early models of incubation energetics suggested that incubation is a period of reduced energy demand compared to other reproductive phases. However, recent studies have shown that the parents sometimes work as hard during incubation as during chick rearing (Tatner & Bryant 1993, Williams 1996). Furthermore, incubation is time-consuming behaviour, thus the incubating parent has limited time to forage for self-maintenance. There is growing evidence that the effort expended during both egg laying and incubation may negatively affect the resources available in later phase(s) of the breeding event, that is, these phases may have a considerable contribution to the cost of reproduction (Monaghan & Nager 1997, Reid et al. 2002).

Waders (203 species, *Charadrii*es infraorder excluding *Laridae*, Sibley & Ahlquist 1990) have an exceptionally high diversity of parental care and mating behaviour (Oring 1982, Székely & Reynolds 1995, Reynolds & Székely 1997). For example, male-only, female-only and biparental care may all occur within one genus. This diversity makes this group highly suitable for formulating and testing hypotheses about costs and benefits of parental care. The influence of different factors on the form and length of care is best studied in those species in which different parental care patterns occur within the species, because these species presumably preserved their ability to respond to different ecological and social circumstances and hereby also to experimental manipulations (Clutton-Brock 1991, Székely et al. 1996). I studied one such species, the Kentish plover *Charadrius alexandrinus*. In the Kentish plover either the male or the female may desert the brood shortly after hatching of the eggs, and thus in some broods biparental care, whereas in others either male-only or female-only care occurs simultaneously within one population (Lessells 1984, Warriner et al. 1986, Székely & Lessells 1993, Amat et al. 1999). Kentish plovers are also amenable to experimental manipulations in the field (Székely & Cuthill 1999, Amat et al. 2000), that makes this species an excellent model system to study parental care decisions.

The main objective of my thesis is to evaluate the various costs and benefits of parental behaviour in the Kentish plover. To put my work in this context, first I overview the theoretical and empirical studies of parental care, and then I focus on

the parental behaviour of Kentish plover in four research papers. In these studies I investigate both the incubation and brood-rearing behaviours. First, using an automatic recording system, I determined the daily pattern of incubation in both sexes. Second, the daily mass change of plovers during incubation was studied by repeated capture of females. Third, I carried out an experiment to find out why both parents incubate the eggs. Finally, I looked into brood-rearing behaviour and asked whether the ecology of brood-rearing habitat may influence the behaviour of parents and their chicks.

Specific objectives

The evolution of parental care

To understand the main issues in the evolution of parental care, I wrote a review on parental care. In this review parental care was viewed from a life-history perspective, and some of the topical issues were investigated such as the single-sex and game-theoretic models of care, the feedback relationships between care and mating systems, the various costs and benefits of care, the influence of paternity on paternal care, and phylogenetic patterns in parental care.

Incubation behaviour in the Kentish plover

Daily routine of incubation.

Previous studies of incubation behaviour were carried out only during the daylight hours in the Kentish plover. To have a full estimate of incubation routines, I constructed an automatic recording system, the transponder system that collected data at the nest over the full day.

Change in body mass during incubation.

To assess the cost of incubation I measured the body mass changes in incubating females at different times of the day. Since body masses are highly variable across females, a set of females was captured and re-weighed repeatedly.

Constraints maintaining biparental incubation.

Why do both parents incubate in the Kentish plover? I carried out a mate-removal and food supplementation experiment to investigate whether a single parent can cope with the demand of uniparental incubation. I predicted that incubation time, i.e. percent of time when the nest is incubated, will decrease in experimentally 'deserted' nests, and the left-alone parent will lose body mass. It has been proposed that a major reason why a single parent is unable to incubate the eggs is

decreased time available for foraging and hereby replenishing energy reserves (Erckmann 1983, Oring 1986). Therefore, I also investigated whether the effects of mate removal can be attenuated by food supplementation.

Brood-rearing behaviour in the Kentish plover

Kentish plovers rear their chicks in two types of habitats in southern Turkey: on the lakeshore and in the saltmarsh. The lakeshore remains wet during the full breeding season, whereas the saltmarsh dries out by late June. Do the ecological changes in these two habitats influence brood-rearing behaviour? To answer this question I investigated the distribution of plover families between these habitats and the reasons of their habitat change. I also studied whether the choice of brood-rearing habitat may influence the behaviour of parents and their chicks.

Methods

Study site

Fieldwork was carried out at Lake Tuzla (36° 43' N, 35° 03' E, see Appendix A), southern Turkey where approximately 1000 pairs of Kentish plover bred around the lake (see Székely & Cuthill 1999, Székely et al. 1999). The vegetation consisted mainly of halophytic plants, such as *Artrochnemum fruticosum*, *Salicornia europaea* and *Sueda prostrata* (Uzun et al. 1995). The study was carried out in an area of approximately 200 ha on the north side of the lake between 1996 and 1999.

Why study Kentish plovers?

The Kentish plover is a small (body mass is about 40-44 g, Appendix B), cosmopolitan, mainly insectivorous wader (Cramp & Simmons 1983). The plumage of adults is dimorphic; the males have black breast-bands and head-stripes, and cinnamon crowns, whereas the upper part of females is pale brown. Kentish plovers breed in sand dunes, saltmarshes and salt pans along the coast, whereas in inland areas they breed in saline grasslands (Meininger & Székely 1997). Their modal clutch size is three. The eggs are deposited in a small scrape and they are incubated by both parents. The eggs hatch after about 25 days of incubation (Appendix C). The chicks are precocial and they feed for themselves. After hatching either parent may desert the brood, although desertion by females is more common than desertion by males. The deserted parent attends the brood until

the chicks fledge at about 28 days. The deserting parent may remate and initiate a new reproduction attempt shortly after desertion (sequential polygamy).

Incubation behaviour

Incubation behaviour was recorded by two methods. Firstly, an automatic recording device (the transponder system) was developed and used in 1997 to record the identity of parents on the nest over full days. The system consisted of a small (0.4 g) passive chip (transponder) glued on the tail feathers of each parent, an antenna buried under the nest and a recording device that was made up of a transponder reader and a palmtop computer. The system was powered by a car battery, and all units of the system were hidden underground. Secondly, the behaviour of parents at the nest was recorded from a hide at about 45-70 m from the nest between 1997 and 1999. Behaviour was recorded for two or three hours using instantaneous scans.

Diurnal changes in body mass

We captured a set of females on their nest three times in 1999: each female was caught once in the morning, once at midday and once in the afternoon. Captures of the same female were carried out on different days and the sequence of captures was randomised to minimise the effect of carry-over.

Mate-removal and food supplementation experiment

By this experiment we tested the ability of parents to incubate on their own. The experiment lasted for four days at a nest. On Day 1 both parents were caught, ringed and measured. On Day 2 the incubation behaviour of parents was recorded. On Day 3 both parents were recaptured, re-weighed and one parent (either the male or the female) was removed at manipulated nests, whereas in control nests both parents were released. On Day 4 the incubation behaviour of the parent(s) was recorded. After the behavioural sample the parent(s) were re-captured and re-weighed, and subsequently the removed parent was released. A small tray was placed near each nest on Day 3, and mealworms (*Tenebrio molitor* larvae) were provided on Day 3 and 4 at supplemented nests, whereas at unsupplemented nests the empty tray was visited at an equivalent number of times.

Plovers were removed for a short period of time to minimise costs imposed on the remaining parent, and to decrease the frequency of nest desertion. Repeated measurements of the same parent enabled us to use each bird as its own control, thus we increased the likelihood of detecting an effect (if it existed). The experiment was carried out in 1998 and 1999.

Brood-rearing behaviour

Individually marked parents and their chicks were followed until the chicks died or reached an age of 25 days in four years (1996-1999). Each brood was visited every other day, and the number and sex of attending parent(s) and the type of brood-rearing habitat were recorded. The behaviour of the family was recorded for one to two hours every 4-6 days. During behavioural samples the type of brood-rearing habitat was also recorded, and ambient temperature was measured at the end of each sample. Density of plovers was estimated during behavioural samples in 1998.

Results

The evolution of parental care

In the review of parental care (Kosztolányi & Székely 2002a) we outlined why there is a conflict over care. We argued that the relationship between parental care and mating systems is not unidirectional, as previously was thought, but rather feedbacks operate between them. A theoretical framework to investigate the bidirectional relationships between mating and parental behaviour was also presented. We investigated the main factors that can modify the extent of care by discussing case studies. For example, we evaluated how the number of young in a reproductive attempt, food availability or remating opportunities may modify the decisions of parents about care.

Parental care is usually approached from two theoretical perspectives: from the perspective of a single-sex (male or female) and from the perspective of the game between parents. Single-sex models investigate how different ecological and behavioural factors may influence the decisions of an individual about care, whereas game-theoretic models consider the decisions of the mate and other members of the population. We explained the logic of a single-sex model and a game-theoretic model in details. Testing of models raises several difficulties, therefore only a few models were tested in the field or in the laboratory. We presented an experimental test of a game-theoretic model in which the operational sex ratio and the benefit of biparental vs. uniparental care were manipulated.

Advances in molecular genetics such as DNA fingerprinting have revealed that the social partner of many females is often not identical with the genetic parent of the offspring, because some offspring may be the result of extra-pair fertilisations (Westneat 2000). The parental care for non-kin offspring is wasted from the viewpoint of cuckolded males, therefore they should guard against this wasted investment. This may be achieved either by preventing extra-pair

fertilisations of the female e.g. by mate guarding, or by adjusting the amount of paternal care according to the actual paternity. However, the results of studies on the relationship between paternity and paternal care are contradictory that can be reconciled by a recent theoretical model (Houston & McNamara 2002).

To understand parental care of contemporary species, it is often instructive to reconstruct evolutionary pathways of care (Székely & Reynolds 1995, Reynolds et al. 2002). Via two examples, we briefly presented how modern phylogenetic comparative methods allow us to reconstruct the transitions between different form of care, and how these methods allow us to analyse ecological and life-history factors that influence the parental behaviour of closely related taxa.

Incubation behaviour

We investigated the incubation behaviour of Kentish plover in three studies (Kosztolányi & Székely 2002b, Szentirmai et al. 2001, Kosztolányi et al. submitted). We found that the transponder system proved as both accurate and reliable in the field (Kosztolányi & Székely 2002b). The percentage of false readings (i.e. when the system was unable to determine whether the male, the female or neither parent was on the nest) was low (0.2% of total recording time). Data collected simultaneously by visual observation and by the system were highly correlated. Therefore, the transponder system was appropriate to determine the daily incubation routines of male and female parents.

Observations and records of the transponder system showed that the eggs were incubated by either parent in 89.4% (median) of time over the day, although there was a significant daily variation: incubation was most intensive at night, early morning and midday. Also, the share between the sexes showed a strong daily pattern: females undertook most of the incubation during daytime, whereas males incubated mostly at night. Overall, females spent more time incubating the nest ($11.3 \text{ h} * \text{day}^{-1}$) than males ($9.4 \text{ h} * \text{day}^{-1}$) during the full day.

Since females carry out the bulk of daylight incubation, we suspected that they may not have enough time to feed and maintain their body condition. Therefore, we investigated the body condition changes of females (Szentirmai et al. 2001). Body mass of incubating females changed over the day: it decreased from morning to midday by 3.4% (median), and from midday to afternoon by 3.7%. The total loss in body mass was 8.4% of the initial mass from morning to afternoon. The body mass loss was significant from morning to midday and from morning to afternoon.

One possible interpretation of the decreasing body mass of females is that incubation is costly in terms of reserves. Why do not female Kentish plovers abandon the clutch similarly to the behaviour of a closely related wader, the dotterel *Eudromias morinellus* (Kålås & Byrkjedal 1984)? The benefits of

desertion during incubation may be twofold: avoiding the cost of incubation, and finding a new mate and renesting shortly after desertion. Thus the question arises, whether the abandoned parent can incubate the eggs on its own, and whether the abandoned parent is able to hatch the eggs.

We investigated this question by a mate-removal and food supplementation experiment (Kosztolányi et al. submitted). After the removal of their mates, males increased their incubation time. This increase, however, did not compensate for the shortfall of their mate, therefore total nest attentiveness was lower at male-only nests (48.1%) than at biparental controls (69.1%). Female incubation was not influenced by the removal of their mate, and thus nest attentiveness at female-only nests (45.7%) was also lower than at biparental nests. We found no difference in incubation behaviour between supplemented and unsupplemented uniparental nests: neither total incubation nor incubation by the male or the female was different.

After mate removal the body mass of males decreased, and their body mass was higher in food supplemented group than in unsupplemented group. However, neither removal nor food supplementation had an effect on female body mass.

Brood-rearing behaviour

Parents shuttled with their chicks between the lakeshore and the saltmarsh, and as the season progressed families spent more time on the shore (Kosztolányi et al. in prep.). This behaviour is likely due to higher prey availability on the shore: chicks pecked for prey in 15.4% of their time on the shore, whereas they pecked only in 6.2% in the saltmarsh. Over the breeding season food availability decreased both for the parents and their chicks in the saltmarsh, whereas it tended to increase on the shore. As food density in saltmarsh decreased, families moved to the shore, and therefore density of families increased on the shore.

The changes in ecology and spatial distribution have induced changes in behaviour. The higher density of plovers on the shore resulted in more fights, because parents had to fight more with neighbouring plovers for feeding territories. Furthermore, the higher densities resulted in longer biparental care on the shore than in the saltmarsh, since females decided to stay for longer with their brood, presumably to defend their chicks from neighbouring families.

Conclusions

The main messages of the parental care review are as follows (Kosztolányi & Székely 2002a). Parental care is a complex trait, thus no single approach such as observations, experiments, theoretical modelling or phylogenetic analyses can

fully address all aspects of this behaviour. To understand the parental care, we need integrative studies that consider several of these perspectives. Furthermore, parental care should be investigated in such a theoretical framework that takes into account the relationships between care and mating behaviour. Current studies of parental care are focussed on the different costs and benefits, and it is assumed that the patterns of care are driven by contemporary selection pressures. Selection can work on a trait only if it is heritable, that is, if it has additive genetic variance. However, little is known about the quantitative genetics of parental care and only few studies had estimated the heritability of care (Freeman-Gallant & Rothstein 1999, Kölliker & Richner 2001).

The field studies reported in the second part of my thesis lead to a number of novel insights. By using the automatic recording system, we were the first who reported the daily pattern of incubation over the full day in the Kentish plover (Kosztolányi & Székely 2002b). Although the incubation behaviour of this species was investigated previously in several studies (e.g. Purdue 1976, Nakazawa 1979, Paton 1995), none of these attempted to quantify incubation behaviour at night. Data on the share of sexes over 24 hours are necessary to reveal the contribution of each sex to incubation. We found daily variation in total incubation that may be explained by ambient temperature, i.e. incubation is more intense if the ambient temperature is extremely high or low (Purdue 1976, Nakazawa 1979). We proposed that sexual dimorphism in plumage via conspicuousness to visually searching nest-predators, or the difference in predator detecting ability between the sexes may explain the different incubation routines of sexes. Thus, further experiments are warranted to determine how and why the costs and benefits of incubation change over the day for each sex. If these costs and benefits are known, we can model how the sexes settle the sexual conflict about parental investment during incubation and how these costs and benefits shape the pattern of incubation.

Our investigation of body mass change revealed that there is a possible cost of incubation in females (Szentirmai et al. 2001). The decrease in body mass may be resulted from depletion of fat reserves and/or evaporation of water. These alternatives require physiological analyses. Depletion of fat reserves may be high in the morning when the ambient temperature is low and therefore an elevated metabolic rate is needed to maintain egg temperature (Williams 1996), whereas water evaporation may be necessary to cool the eggs at high temperatures e.g. at midday. Furthermore, cooling the eggs may also elevate the energy expenditure of the parent (Hinsley & Ferns 1994). These considerations suggest that body mass loss may be an indication of the cost of reproduction (Roff 1992), although we cannot rule out strategic mass regulation (Moreno 1989, Witter & Cuthill 1993, Thomas 2000).

An interesting and puzzling idea was recently proposed by Barta et al. (2002). They showed that females may strategically manipulate their own condition in a

game-theoretic context to ‘force’ their partner to stay with them. Once their mate decides to care then the females may desert, and thus exploit the males’ decision. This prediction needs experimental tests to reveal whether incubating plovers may strategically manipulate their own body condition to extract more care from their mate.

The results of our mate-removal and food supplementation experiment suggest that the costs of uniparental desertion during incubation are probably higher than during brood rearing (Kosztolányi et al. submitted), since the total incubation time decreased after removal of one parent. Even if a single parent can keep the temperature of eggs within the required range for normal development and the viability of eggs does not decrease, the development of embryos should still slow down at uniparental nests. Therefore, the length of incubation period should increase, that in turn increases the risk of nest predation (Webb 1987). Furthermore, the deserted parent may simply terminate the incubation, and thus doom the offspring to death.

However, food supplementation did not have the predicted effect on incubation behaviour. We propose that either the type of supplementary food was not sufficiently diverse (Slagsvold & Johansen 1998), or the energetic requirements are not the main driving force behind incubation schedules in the Kentish plover.

By investigating the movements of broods (Kosztolányi et al. in prep.), we showed that families move between the habitats, and suggested that the difference in food availability explains the habitat choice. This conclusion is similar to the one drawn from the study of the piping plover *Charadrius melodus* in which parents with their chicks choose the habitats where the arthropod abundance is high (Elias et al. 2000). As an effect of the movements of broods, the density of plovers increased on the shore, and this in turn influenced their behaviour, and the length of biparental care. However, it remains to be shown why some families decided to stay in the less profitable saltmarsh, whereas most others moved to the shore.

Taken together, we showed that the incubation pattern of males and females in the Kentish plover are different. This pattern is similar to other plover species in that the females incubate mostly during daylight, whereas the males are on the nest at night (Thibault & McNeil 1995, Warnock & Oring 1996, Blanken & Nol 1998). We also found that incubation is an apparently costly behaviour. However, the results of an experiment suggested that the costs of desertion during incubation may be high. Furthermore, we showed that the parents choose between the brood-rearing habitats depending on food availability, and that the pattern of parental care may be influenced by the ecological and social changes in the brood-rearing habitats.

My results and those included in the PhD thesis of Kis (in prep.) are aimed at understanding how costs and benefits of parental care may influence the pattern of care. Our ongoing studies in the Kentish plover investigate in particular, whether mating opportunities may influence care patterns. The results suggest that this may be the case. First, it was shown that females desert their broods more often than males (Székely 1994). Second, this pattern is consistent with the explanation that the mating opportunities of males are worse than that of females (Székely et al. 1999). The biased mating opportunities may be the results of biased chick sex ratio or different survival of the sexes. Using molecular sexing recently we showed that the sex ratio at hatching does not differ from unity, although the survival of daughters until fledging was lower than that of sons (Székely et al. in press). Also, late broods had more daughters than sons, and previously we showed higher mortality in late broods (Székely & Cuthill 1999). Furthermore, in a study using mark-recapture methods, we found that the survival of adult males and females is not different (Sandercock et al. submitted). Thus, both the lower pre-fledging survival of females and the higher mortality of late broods may result in male biased adult sex ratio. This bias in turn may explain why females remate faster than males, and thus it may explain the enigma of female-biased brood desertion.

In conclusion, the Kentish plover is an excellent model system to investigate various costs and benefits of care. My studies produced a number of novel results in both incubation and brood-rearing behaviour. However, many questions have remained to be answered. In my view, the most interesting aspect of parental care is the solution of sexual conflict. What is the process of caring/deserting decisions? One sex decides first and the other only goes with this situation, or the decisions are results of long negotiation processes between the sexes? Is the share of the two parents constant after this negotiation process, or there is a continuous debate between the parents about the care? To answer these questions we need new game-theoretic models of parental care, and field-based experiments to test the predictions of the models.

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Publications

Publications and manuscripts included in the thesis

- Kosztolányi, A.** & Székely, T. 2002a. The evolution of parental care. In: New Directions in Behavioural Ecology (Barta, Z., Liker, A. & Székely, T., eds.). Osiris, Budapest, pp. 97–116 (in Hungarian).
- Kosztolányi, A.** & Székely, T. 2002b. Using a transponder system to monitor incubation routines of snowy plovers. *Journal of Field Ornithology* 73: 199–205.
- Szentirmai, I., **Kosztolányi, A.** & Székely, T. 2001. Daily changes in body mass of incubating Kentish plovers. *Ornis Hungarica* 11: 27–32 (in press).
- Kosztolányi, A.**, Székely, T. & Cuthill, I. C. Why do both parents incubate in the Kentish plover? *Ethology* (provisionally accepted).
- Kosztolányi, A.**, Székely, T. & Cuthill, I. C. The influence of habitat on brood-rearing behaviour in Kentish plover (manuscript in preparation).

Related publications and manuscripts

- Sandercock, B. K., Székely, T. & **Kosztolányi, A.** The effects of age and sex on the survival of Kentish plovers (*Charadrius alexandrinus*) breeding in southern Turkey. *Ibis* (submitted).

Published conference abstracts

- Kosztolányi, A.** & Székely, T. 1999. Incubation behaviour of Kentish plover *Charadrius alexandrinus*. *Wader Study Group Bulletin* 88: 10.

Talks and posters

- Kosztolányi, A.** & Kisdi, É. 1996. Optimization of life histories in energy structured populations (poster). Vth International Congress of Systematic and Evolutionary Biology, Budapest.
- Kosztolányi, A.** 1997. Optimization of life histories in energy structured populations (talk in Hungarian). XXIII. OTDK, Nyíregyháza.
- Kosztolányi, A.** 1998. Incubation patterns in the Kentish plover (talk in Hungarian). Data Processing and Statistical Methods in Ecology and Behavioural Ecology, Postgraduate Course, Budapest.

- Kosztolányi, A. & Székely, T.** 1998. Incubation behaviour of Kentish plover *Charadrius alexandrinus* (talk). Wader Study Group Annual General Meeting, Keszthely.
- Kosztolányi, A.** 1999. Incubation behaviour of Kentish plover *Charadrius alexandrinus* (talk in Hungarian). New Directions in Behavioural Ecology, Postgraduate Course, Debrecen.
- Kosztolányi, A. & Székely, T.** 1999. Incubation behaviour in the Kentish plover (poster). 117th Meeting of the American Ornithologists' Union, Ithaca.
- Kosztolányi, A. & Székely, T.** 1999. Incubating behaviour in the Kentish plover (talk in Hungarian). Vth Scientific Meeting of the Hungarian Ornithological and Nature Conservation Society, Budapest.
- Kosztolányi, A. & Kis, J.** 2000. Mating systems and parental care in waders (talk in Hungarian). Meeting of the Hungarian Biological Society, Section for Zoology, Budapest.
- Kosztolányi, A.** 2001. Why do both parents incubate in the Kentish plover? (talk in Hungarian). Meeting of the Hungarian Ecological Society, Budapest.
- Kosztolányi, A.** 2002. The influence of habitat on parental care in the Kentish plover (talk in Hungarian). Models in Behavioural Ecology, Postgraduate Course, Debrecen.
- Kosztolányi, A., Székely, T. & Cuthill, I. C.** 2002. The parents' dilemma: where should they rear their young? (poster) First European Conference on Behavioural Biology, Muenster.

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Research papers

1.

The evolution of parental care

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Summary

Parental care is often a time and energy demanding behaviour, nevertheless many animals exhibit some form of care. The form of parental care may be different not only between higher taxa but even between populations, sexes or individuals. In this chapter, firstly we review the diversity of care in conjunction with mating systems. Second, we investigate the factors that may influence the costs and benefits of parental care, and hereby determine whether a parent cares for its brood or not, and if it does then how much care she/he will provide. Third, we outline an optimisation model and a game theoretical model of parental care. We review the testability of models and the problems of testing, and we present a specific test of a game theoretical model. Fourth, we examine how paternity may influence paternal care. Finally, we present the results of a recent study that used the comparative phylogenetic methods.

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Introduction: why do parents take the trouble of caring for their offspring?

There are various forms of parental care in the animal kingdom (Clutton-Brock 1991). Mammals lactate their offspring, whereas most birds incubate the eggs, and many of them protect, brood and feed the hatchlings. Parental care is not a privilege of higher vertebrates, for example, some frogs carry the tadpoles on their back to secure the survival of offspring, and parents of a cichlid fish (*Symphyodon discus*) nourish their young with an ectodermal mucus. Parental care is rare among invertebrates. The obvious exceptions are the social insects (ants, bees, wasps). Furthermore, burying beetles (*Nicrophorus*) prepare small balls from carcasses of animals, bury them underground and oviposit in them. These balls provide food for hatched offspring.

Not only the form of care, but the sex of caring parent also shows variation across taxa. In mammals, generally only the female cares, whereas in fishes male care is very common, and birds have typically biparental care (Krebs and Davies 1993). The sex of the caring parent may also vary between closely related taxa. For example, biparental care is the most common type of care in waders (*Charadrii*), although several waders exhibit male-only and female-only care (Székely and Reynolds 1995).

Furthermore, the length of care may also vary. Some mammals and birds care for their offspring for months, occasionally for years; for instance, Oystercatcher chicks (*Haematopus ostralegus*) are fed by parents up to a half year. Several primates and carnivores rear, teach and protect their offspring for a number of years.

Why do parents spend so much time and energy on rearing their young? Before we answer this question, we need to give several definitions. Any parental behaviour that increases the survival prospects of offspring may be considered parental care (Clutton-Brock 1991, Clutton-Brock and Godfray 1991). In this sense, parental care may not entail costs for the parent(s). In contrast, Trivers (1972) defined parental investment as any parental behaviour that increases the survival prospects of an individual offspring, and decreases the investments of the parent into other offspring. That is, parental investment increases the benefit from current offspring at the cost of the decrease of the future reproductive prospects of the parent (Roff 1992). Parental investment may not be proportional to the resources devoted to offspring e.g. energy (Trivers 1972). Imagine a parent protecting its offspring from predators. The parent may only invest small amount of energy for defence, although its behaviour could have considerable effect on its future, since brood-defending parents may be eaten by the attacking predator.

The investigation of parental care is important from several aspects. Firstly, since parental care or parental investment may entail costs (cost of reproduction, Williams 1966), the investigation of parental care/investment is necessary to understand the life history evolution of the organisms (Roff 1992). Secondly, the sex of the caring parent and the length of care may influence which mating system develops (Reynolds 1996, Székely et al. 2000b). Thirdly, parental care is often a joint decision of both parents, therefore it provides an excellent opportunity to develop and test game theoretical models. Lastly, parental care is of key importance in reproductive success of many animals. Thus, existence or absence, quality and form of care may radically influence the population dynamics and conservation biology of animals.

Parental care and mating systems

For a long time it was thought that parents collaborate harmonically during the period of raising their young, because seemingly both parents have the same goal, that is, to produce as many descendants as possible. Trivers (1972) was the first who recognised that there may be a conflict of interest between the parents over care, since there are situation when it would be more profitable for both parents if the other parent rears the offspring. By abandoning the offspring, i.e. by desertion parents may gain, because on the one hand they are released from the burden of care, and on the other hand they are able to spend time and energy on searching for new mates and on other reproductive attempts. Therefore, offspring desertion (e.g. nest or brood desertion), which had been thought abnormal previously, may be adaptive in many cases (Székely et al. 1996).

Following Trivers' (1972) argument, the decision of parents between care and desertion is influenced by investments up to the given time. The sex caring more (typically the females) becomes limiting for the other sex, thus the parental investment directs sexual selection, and mating system evolves in response to the care pattern adopted by the population.

However, this argument is false, because not past investments should count, rather the animals should maximise the number of descendants they are expected to produce in future (Dawkins and Carlisle 1976). Dawkins and Carlisle called the logical flaw in Trivers' argument as 'Concorde fallacy' referring to the flawed decision of the British and French governments to continue the Concorde program, even when it became evident that the Concorde airplanes will never be profitable. They used the faulty argument that if so much has been invested into the Concorde program, then it is worth finishing it. Thus, the reason for completing brood care of a nearly independent offspring is not because the parent(s) have already invested a lot in rearing the young (Trivers' argument), but because the continued

investment gives better costs/benefits ratio than beginning to rear a new batch of young (Dawkins and Carlisle's argument).

Two classic papers, both published in 1977 investigated the relationship between parental care and mating systems. On the one hand, Emlen and Oring (1977) thought that parental care influences the ratio of fertile females and of sexually active males (operational sex ratio, OSR). For example, if in a population most females care for their offspring, then only few females are available for matings. Therefore, the OSR is biased toward males and a strong competition is expected for the access to females. The more biased the OSR, the more intense is the sexual selection. The OSR with the spatial and temporal distribution of resources determine which mating system emerges in the population. Thus, in the Emlen and Oring's schema, parental care influences the mating system through the OSR (Fig. 1. A). On the other hand, Maynard Smith (1977) approached the relationship between mating systems and parental care from the side of parental care, because he thought that mating opportunities determine whether or not an individual cares for the offspring and if yes, how long it cares. The probability that a deserting parent finds a new mate depends, in turn, on OSR. Therefore, following Maynard Smith's logic, the OSR should influence the mating system (Fig. 1. B). There have been separate research programs and models built on these two opposite approaches up to the nineties (see Davies 1991, Lazarus 1990).

However, the relationship between care and mating systems may be not unidirectional, rather feedbacks may operate (Reynolds 1996, Westneat and Sargent 1996). Therefore, the investigation of mating behaviour and parental care cannot be separated; they and their interactions have to be investigated in a single theoretical framework (Fig. 1. C, Székely et al. 2000b). For example, mating opportunities influence how paired and unpaired individuals behave, whilst decisions about mating and parental care influence mating opportunities. The environment (e.g. the distribution of resources and the intensity of predation) may influence both mating and caring decisions. Testing this new theoretical framework is a promising avenue of future research.

Factors influencing the decisions of parents

The theory of life-history evolution assumes that parents devote their resources to care in such a way as to maximise the number and quality of their descendants, that is, their own reproductive success during their lifetime (Clutton-Brock 1991). The extent of parental expenditure, like the extent of any expenditure, is controlled by the entailing benefits and costs. These costs and benefits, and thus the parental decision are influenced by the state of the parent and offspring, as well as the state and behaviour of the mate and other members of the population (Houston and

McNamara 1999). The decision of a parent may not only be quantitative, i.e. increase or decrease care but also qualitative, i.e. abandon the offspring before independence. For example, in several fishes and birds one or both parents desert the offspring. Female mammals may abort the foetus, and the litter may be resorbed in the uterus or parents may eat the newborns (Clutton-Brock 1991, Székely et al. 1996).

Since the primary benefit of parental care is increased offspring survival, the care should relate to the expected reproductive value of offspring. The number of descendants produced in one reproductive attempt may determine how much benefit is expected from rearing of young. If there are only a few young to rear, reduced care is expected, whilst in the opposite case more care is expected. Observational studies showed that in birds small clutches are more often abandoned than large ones (Székely et al. 1996). For example, the nest desertion of female Collared flycatcher (*Ficedula albicollis*) is significantly related to her clutch size (Wiggins et al. 1994). However, the different individual qualities of carers and deserters may confound the results of observational studies. For instance, if females laying small clutches are in worse condition than other females, they probably desert more likely the offspring as well, independently of the clutch size (phenotypic correlation). However, experimental studies confirmed the causal relationship between the number of offspring and intensity of care: by enlarging clutches, the intensity of care increased in several fishes and birds (Clutton-Brock 1991), whereas after an experimental reduction of clutch size, the parents usually gave up care (Székely et al. 1996, Jennions and Polakow 2001).

If the expected survival of offspring is low despite of care, then reduced care and/or desertion are expected. For example, if there is low food availability, the rearing of young is not secured. For instance, White pelicans (*Pelecanus erythrorhynchos*) desert more than 75% of nests in certain years, and desertion is presumably caused by low food availability (Johnson and Sloan 1978). Likewise, White ibises (*Endocinus albus*) abandon their hatchlings, because the food appears to be scarce (Bildstein et al. 1990). However, the relationship between food availability and offspring desertion may also be the opposite. The Snail kite (*Rostrhamus sociabilis*) is a food specialist raptor that feeds itself and its young almost exclusively on an aquatic snail species. One parent typically deserts the offspring, and the deserted parent rears the hatchlings alone (Beissinger and Snyder 1987). The frequency of desertion depends on food availability: if there is plenty of food, one parent alone is able to carry enough food to hatchlings, therefore the other parent may desert without risking the survival of offspring. Desertion may also take place if there is too little food. In the latter case both parents cease incubation or even brood rearing. The difference in the bidirectional relationship between food availability and offspring desertion is that after

desertion by both parents the hatchlings die, whereas after desertion only by one parent the hatchling will survive at a relatively high chance.

The survival prospects of offspring may be lowered by parasite infection. For example, the nest or hatchling abandonment increased when the nest was infected artificially by blood sucking parasites in the Great tit (*Parus major*, Oppliger et al. 1994).

A positive relationship is expected between the genetic relatedness of the offspring to their parent and parental care, because each individual should invest in offspring bearing the parent's genes. However, males Fathead minnows (*Pimephales promelas*) do not seem to behave optimally (Unger and Sargent 1988). This fish oviposits on the underside of rocks in streams and the male protects the fertilised eggs. Since appropriate oviposition sites are in short supply, males compete for them, and sometimes a male protecting its fertilised eggs is chased away from its territory. In these cases the newcomer does not kill the offspring of the previous male, but it defends them in spite of it being costly. The benefit of these males is nevertheless more than the cost of caring for foreign offspring, because females find egg-guarding males more attractive than non-guarding ones (Unger and Sargent 1988). In birds reduced relatedness may be the result of intra- or interspecific brood parasitism and/or extra-pair fertilisation. In the former, both parents' relatedness with the offspring decreases, whereas in the latter only that of the male.

In iteroparous animals, that is, in animals reproducing more than once in their life, reproduction may be more costly for young parents than for old ones. The reason for this difference may be that young animals may spend more time and energy on raising their young, for instance, because they do not have enough experience about the distribution of food and/or about avoiding predators. Furthermore, reproduction decreases the residual reproductive value, and this reduction is more costly for younger individuals (Clutton-Brock 1991). For example, the fecundity of female fishes increases exponentially with body size. Therefore, if a young and small female invests too much in its offspring, it pays a high price, since its future reproductive success decreases considerably. This is one of the proposed explanations why the male care is more common than the female care in fishes with parental care (Alcock 1998).

A parent in a low body condition should decrease care or cease provisioning altogether to ensure its own survival and future reproduction. There are several examples for the connection between low parental condition and offspring desertion in birds and mammals (review: Clutton-Brock 1991, Székely et al. 1996). The reason for offspring desertion may not only be the increasing parental condition and survival. For example, in polygynous Great reed warblers (*Acrocephalus arundinaceus*) some male leave its territory before offspring become independent (Urano 1992). The survival of deserting and caring males

does not differ, because they return with the same rate from the wintering site on next spring. However, males deserting in previous year return earlier that increases their chances of finding a better breeding site, and thus they can mate with more females (Urano 1992). Thus, male Great reed warblers increase their future productivity by terminating care. However, we should bear in mind that another possible interpretation of Urano's (1992) result is phenotypic correlation (see above): good quality males exhibit desertion behaviour and also they acquire more females because of their inherent characteristic. Thus, a causal relationship between frequency of desertion and future reproductive success is not the only viable explanation.

However, the benefit of desertion may not only arise in the future reproductive cycle. If there are individuals suitable for mating in the population, the deserting individual can remate, and thus increase the number of descendants. In Penduline tits (*Remiz pendulinus*) usually only one parent takes part in parental care. For example, in Sweden 48% of nests are cared for only by the female, 18% are cared for only by the male, and 48% are deserted by both parents. Parents deserting their offspring search for a new mate and begin to build a new nest (Persson and Öhrström 1989). Remating also occurs in the Kentish plover (*Charadrius alexandrinus*). After hatching of the precocial chicks one parent, usually the female, leaves the family and searches for a new mate (Székely and Lessells 1993). The chicks are cared for by the parent left alone until the chicks are independent, although there are families in which both parents remain with the chicks (Székely and Cuthill 2000).

Retention of the mate may also increase reproductive success. For example, female Barnacle geese (*Branta leucopsis*) incubate alone, but their mates defend the nest and also guard the hatchlings. Pairs breed usually together for several years and remain together on the wintering site. Black et al. (1996) showed that the long partnership is beneficial for Barnacle geese pairs, because the number of goslings reared during a breeding season increased with the length of partnership, independently from the age of individuals.

Models of parental care

Since the seventies theoretical biologists are developing mathematical models to understand the diversity of parental care. These models approach the problem in two ways. One class of the models focuses on the behaviour of one individual (or sex) and investigates the effect of different ecological and behavioural factors on parental care (single-sex models, e.g. Carlisle 1982, Kelly and Kennedy 1993). The other class of models is game theoretical. In the latter models, the behaviour of individuals is investigated in conjunction with the behaviour of the other parent

and/or other members of the population (e.g. Maynard Smith 1977, Houston and Davies 1985, Lazarus 1990). Here we illustrate these two approaches by an example of each.

Single-parent model: parental behaviour in relation to current and future benefits

Carlisle (1982) compares the fitness of current and future offspring. The value of current offspring (B) increases with the resources invested in the offspring (c), whereas the value of future offspring (F) decreases with the care devoted to current offspring (cost of reproduction). The units of functions B and F are fitness units, and the shape of these functions is determined by environmental factors. Parental care is optimal (c^*) if the parent maximises its fitness, that is, it maximises the sum of its current and future reproductive success, $B(c) + F(c)$.

If both B and F are linear functions of c , then there is either no parental care, or care is maximal depending on the slope of these functions. For example, if the slope of B is higher in absolute value than that of F (Fig. 2. A), function $B(c) + F(c)$ is increasing. Therefore, the parent has to invest in offspring as much as it can ($c^* = C$, where C is the maximum of resources expendable on the offspring). In the opposite case (Fig. 2. B), function $B(c) + F(c)$ is decreasing, therefore even small parental care decreases the fitness of the parent, thus no care is expected. To observe a parental care with intermediate level of parental effort ($0 < c^* < C$), at least one of the functions has to be non-linear, and the slope of B has to be steeper than that of F at point $c = 0$ (Fig. 2. C). Thus, the model gives qualitative prediction (cares / does not care) in case of linear functions, whilst it gives quantitative prediction (How much it cares?) in case of non-linear functions.

This model, despite of its simplicity, can be applied to answer certain questions. For example, how should the investment of a parent change if there is more than average food available during the period of parental care? In this example we suspect that the slope of B increases, because the survival of offspring is ensured with less expenditure, as less time and energy are needed to gather a given amount of food and to convert it in the fitness of offspring. If the high level of food does not increase the survival or future reproductivity of the parent, then the shape of function F does not change. Under these circumstances, the optimal decision of the parent is to increase the amount of resources invested in the offspring (Fig. 2. D, c_2^*).

The game between parents: care in the Dunnock

The Dunnock (*Prunella modularis*) is a small passerine with diverse mating system and parental care. Dunnocks breed in forests in Hungary, although in

England they often nest in parks. Davies (1992) observed that not only pairs (monogamy) exist in a population, but also one female may mate with several males (polyandry), and one male may mate with several females (polygyny). He studied the Dunnocks in the Cambridge University Botanic Garden, where pairs and trios (one female with two males) were the two most common mating patterns in a ten years study (Davies 1992). In trios, one male (α male, usually the older) was dominant over the other male (β male). In the latter mating system, either only the α male, or both males copulated with the female. If both males copulated, then on average 60% of copulation was performed by the α male and 40% by the β male. In pairs, both sexes fed the young, whereas in trios the female, and either only the α male or both males fed the young. In trios, the β male only fed the young if he copulated with the female. Houston and Davies (1985) modelled the parental care of monogamous pairs and polyandrous trios using a game theoretical model.

In the Houston and Davies model, the relationship between parental investment and expected number of surviving offspring has a saturation function. Parental investment has an initially critical value under which the benefit from offspring equals zero. The shape of gain function depends on clutch size, investment of the other parent(s), food availability and percent of offspring fertilised by the given individual. The relationship between parental expenditure and parental survival is a decreasing function, which depends on parental investment and on terms independent of care. The sum of these two functions (number of offspring and parental survival) gives how many descendants a parent will have. That is, how many offspring are expected to survive until the next breeding season, and what the probability is that the parent itself survives. The optimal amount of care maximises this sum. The optimal amount of investment can be found by differentiating. To keep the maths simple, the researchers chose the parameters of functions in such a way that the optimal investment of a parent, i.e. its best response to the investment of the other parent gives a linear function (Fig. 3. A and 3. B). To find the conditions when the parents cooperate, we need to find the evolutionarily stable strategy (ESS). That is, the pair of strategies (E_m and E_f) for which the benefit of males is the highest if they play strategy E_m as long as females play strategy E_f , and the benefit of females is the highest if they play strategy E_f as long as males play strategy E_m . Thus, neither parent has incentive to deviate from the pair of strategies E_m and E_f .

For two parents it is relatively easy to find the pair of investments where biparental care is expected. Both parents will care, if the best responses of the parents cross, and their slopes are less than -1 (Fig. 3. C). Thus, the intersection is an ESS, because the investment of a parent increases if the investment of the other parent decreases, although this increase does not fully compensate the decrease. Therefore, the extent of investments converges back to the intersection (see points

1, 2, 3 and 4 on Fig. 3. C). If the two functions do not cross, female-only or male-only care evolves depending on which function lays higher (Fig. 3. D and Fig. 3. E). If the two functions cross, but their slope is greater than -1 , then the intersection is not stable, because the response of a parent to a decreased investment of the other parent is overcompensation, that is, it increases its investment more than the other parent decreases. Thus, the point given by the investment of parents moves away by larger and larger amounts from the intersection until it reaches either axes and only one parent will care. In these cases, it depends on the initial conditions whether male-only or female-only care evolves (Fig. 3. F). If there are three individuals (female, α and β males), the graphical representation is not straightforward, because the investments of individuals should be represented in three dimensions. The intersection of the three planes can easily be found algebraically, although we do not mention the solution here.

The parameters of the model were chosen by A. Houston and N. Davies to coincide approximately with values measured in the Dunnock. In trios the β male was also able to copulate with the female. Qualitative predictions of the model were not sensitive to values of parameters and coincided with the observed extent of care in pairs and trios. For example, parental care of parents increased with increasing clutch size. In trios, care by females was the highest, care by α males was somehow lower, and care by β males was the smallest. The parental care of females was approximately the same in pairs and trios, whilst the parental care of α males was higher in pairs than in trios. We note that the above explanation of Houston and Davies (1985) is simplified, see McNamara et al. (1999) for details.

Models and the reality: testing models

Several care models are general (e.g. Maynard Smith 1977, Carlisle 1982, Lazarus 1990), although there are species-specific models too (e.g. Houston and Davies 1985, Kelly and Kennedy 1993). General models illustrate concepts and trends, therefore it is not advisable to test them directly in a specific animal system. In contrast, species-specific models are parameter-loaded, therefore it is often difficult to solve them and to gain precise predictions. Thus, it may be difficult to compare these predictions with parental care observed in populations. A further problem with model-testing is that the conditions found in contemporary populations may be different from conditions that have occurred during the evolution of care patterns (Clutton-Brock 1991). Therefore, the predictions of a model may not be correct, because we did not take into account (or were not able to take into account) the past conditions. We should also consider that we do not know the specific shape of many theoretical functions in the models. Results of field and laboratory studies can usually be described by several mathematical

functions, whereas the predictions of models often depend on the chosen function. For these reasons, only few models were tested in the field or in the laboratory. For example, in birds, which is perhaps the most often studied taxon, parental care models were tested only in a handful of species (review: Székely et al. 1996).

The most suitable species for experimental testing of models are species that have a great variety in their parental care (e.g. both uniparental and biparental care occur), because these species have presumably preserved their ability to respond to a range of costs and benefits. Such species are for example among birds the above mentioned Penduline tit, Kentish plover and Dunnock, or in fishes the St. Peter's fish (*Sarotherodon galilaeus*) that lives in rivers and lakes of Africa and Asia Minor.

In St. Peter's fish, biparental, male-only and female-only care all occur in the same population. Balshine-Earn and Earn (1997) prepared a game theoretical model for the care of this mouth brooding cichlid. Since the breeding season is long or continuous in the range of St. Peter's fish, the model assumes continuous breeding. The input variables of the model are the proportion of males and females in the population that care for offspring, and the output variable maximises the number of offspring produced per day. The parameters of the model are the OSR, the time that elapses between two broods, and the number of surviving offspring as a function of the number of caring parents. Substituting the values of parameters measured in the studied population, the model predicted male-only care as ESS. However, the frequency of male-only care was low in the population. One reason for this may be that the population has not yet reached the ESS. Another possible reason is that two parameters of the model (OSR and the benefit of biparental care vs. uniparental care) are highly variable, for instance, OSR varied highly in the studied population both in time and space. Furthermore, the OSR found in the field may not correspond to the natural OSR, because the lake was supplied by a male-biased fish stock. Furthermore, the number of fries is highly variable that may influence the advantage of biparental care (P_2) against uniparental care (P_1), since few fries can be easily taken in the mouth by only one parent, whereas many fries require the mouth cavity of both parents. Analysing the model in the whole range of these two parameters, any caring types may be an ESS (Fig. 4).

Several care types may be present in the population if the studied population is in the mixed strategy section of the parameter space, that is, both males and females desert with a given probability. Alternatively, it is possible that individuals decide facultatively about caring based on the current values of the two parameters. Balshine-Earn and Earn (1998) investigated experimentally the latter explanation. They set different sex ratios of fish kept in aquaria, and observed the effect of sex ratio on the type of care. It was difficult to alter the benefits of biparental care against uniparental care, because manipulating the number of fries

would highly disturb the spawning process. Therefore, the body size of males was manipulated: males smaller than females, equal to females or bigger than females were placed in the aquaria. The buccal cavity increases with body size, and thus the advantage of biparental care against uniparental care increases.

The results of the experiment were consistent with the predictions (Fig. 4). At a female-biased sex ratio, the males abandoned their offspring more frequently, and thus the frequency of female-only care increased. In contrast, the frequency of male-only care increased at male-biased sex ratio. Finally, small males abandoned the offspring more frequently than large ones, which was consistent with the prediction that the advantage of biparental care was small.

Paternity and paternal care

In biparental care, the conflict between sexes may be more complicated because of the different genetic relatedness between parents and their young. Novel techniques of the last decade in molecular biology (e.g. gel electrophoresis, DNA fingerprinting) proved that in many birds the brood may contain young fertilised by foreign males as a result of often observed extra-pair copulations (EPCs) (Birkhead and Møller 1998, Boag and Ratcliffe 2000). In these cuckolded broods, the paternal care increases the survival of foreign offspring as well, therefore males should somehow guard against their wasted investment (Trivers 1972). The male prevents the fertilisation by foreign males often by guarding his female or by frequent mating. Alternatively, he may adjust the amount of his care to the percent of offspring sired by him (Birkhead and Møller 1998). However, to adjust the male should have some information about the relatedness between the offspring and itself.

The relation between paternity and paternal response depends on how an individual can estimate its paternity (Westneat and Sherman 1993). If males can accurately assess their paternity, then they can adjust the extent of their care (facultative response). The facultative response may depend on whether the individual recognises its own descendants (discriminant response), or it decides about the extent of care based on indirect cues (indiscriminant response). For example, male Dunnocks appear to use an indirect cue to adjust the extent of paternal care in trios, since they care according to the time the female spent solely with them during the fertile period (Davies 1992). If male Blue-footed boobies (*Sula nebouxii*) were removed during the fertile period, then after returning to the female, the males ejected the eggs laid during their absence presumably, because they were concerned about the faithfulness of their female (Osorio-Beristain and Drummond 2001). However, if males use indirect cues, then females are expected

to play a counterstrategy that decreases the reliability of the cue (Westneat and Sargent 1996).

Contrary to indiscriminant response, no study yet detected discriminant response i.e. a response that is based on the recognition of the own offspring (Westneat and Sargent 1996). It is not surprising, because selection expected to operate against the emergence of discriminant cues that may allow the males to recognise their own offspring. Since offspring indicating the identity of their father would be not cared for by unrelated males, and thus the survival prospects of such offspring would be smaller than that of offspring not indicating their identity (Wright 1998).

If there is no possibility or it is not beneficial to assess the paternity, the extent of care may fixate on evolutionary scale, thus the extent of care may change according to the expected paternity of the current reproductive attempt (nonfacultative response, Westneat and Sherman 1993). In nonfacultative response expected paternity may be based on cues such as the age or the rank of the father (Wright 1998).

Comparing the relationship between paternity and paternal care in birds, Møller and Birkhead (1993) and Møller and Cuervo (2000) found that nestling provisioning by males negatively relate to the frequency of extra-pair fertilisations, and they did not find any relationship between incubation and paternity. On the contrary, Schwagmeyer et al. (1999) using a partly overlapping dataset and slightly different statistical methods found a relationship only during the incubation period. However, not only the results of comparative studies are contradictory. In observational and experimental studies, several researchers found relationship between paternity and paternal care, while others did not for which there may be several reasons (Westneat and Sargent 1996, Wright 1998).

For example, the results of observational studies may be confounded by the different qualities of males. If the paternity of low quality males (e.g. small males or males in bad condition) is lower over their whole lifespan than that of males of good quality, and furthermore these males are less attractive to females in EPCs than males of high quality, then males of low quality are not expected to alter the amount of their care according to their paternity and to invest rather in EPC or survival, because the expected benefit over their whole lifespan is independent of their decision (Westneat and Sherman 1993). The quality of individuals may increase with age, as their size or their experience increases. Furthermore, old males may be obviously of better quality, because usually only high quality individuals survive. Therefore, the paternity of older males may be higher than that of younger males. In such cases, the emergence of nonfacultative response is expected, and thus males are expected to decide about the extent of care based on their age and not on their current paternity (Wright 1998). In the latter situations the extent of care will not be altered if paternity is experimentally manipulated. In

experimental studies the frequency of EPC or the information of the male about the frequency of EPC is manipulated by removal of either sex for a short time during the fertile period of the female. However, it is not sure that these manipulations influence the decisions of males as expected by the researchers (Wright 1998). Furthermore, even if the experiment influenced the males' information about their certainty of paternity then it is still not sure that any effect will be found. For instance, if the function between paternity and paternal care is a saturating curve, then manipulating paternity at the saturating part of the curve may result in small and/or immeasurable response in male behaviour (Wright 1998).

The phylogeny of parental care

As we mentioned earlier, it is often a good idea to know the evolutionary past of parental behaviour. The rapid spread of comparative phylogenetic studies is underpinned by discoveries in two fields of science. Firstly, phylogenetic connections between species and taxa are increasingly better estimated using rapid molecular methods such as DNA hybridisation and DNA sequencing. Secondly, various novel mathematical tools (e.g. statistical methods, computer simulations) were developed to deal with the comparative analyses of species (comparative phylogenetic methods, Harvey and Pagel 1991, Martins 1996).

Székely and Reynolds (1995) studied the phylogeny of the diverse parental care in waders using some of the comparative methods. They constructed the phylogenetic hypothesis of waders using the DNA-DNA hybridisation of Sibley and Ahlquist (1990) and other phylogenetic data. They collected data on the parental care of as many wader species as possible from the literature, and reconstructed the phylogeny of parental care in waders (Fig. 5). The character reconstruction was carried out using parsimony, so that the simplest phylogenetic connections between taxa were searched for (Harvey and Pagel 1991).

Inspecting the reconstructed phylogenetic tree (Fig. 5), it can be seen that the ancestral form of parental care in waders was biparental, although during the evolution various transitions have occurred. In an early stage of evolution a dichotomy occurred. In the parvorder of plovers (*Charadriida* i.e. plovers, stone-curlews and avocets) the biparental care remained, but later also uniparental male care has appeared. Whereas in the parvorder of snipes (*Scolopacida* i.e. snipes, godwits and sandpipers), there was an early evolutionary change to the male-only care, and later biparental and female-only care also evolved several times. The study showed that the frequency of evolutionary transitions among the main types of parental care (biparental, female-only, male-only care) is different. For

example, the change between male-only and biparental care was frequent, whereas the change between female-only and biparental care was rarer.

The other type of comparative phylogenetic methods analyses how ecological and life-historical factors may influence behaviour. One of the main problems with previous comparative studies was that the researchers carried out statistical analyses by assuming that all species were separate data points. However, the behaviour of close related species is usually very similar, therefore it is not correct to use conventional parametric and nonparametric statistics for the obviously not independent data points. New phylogenetic comparative methods applying contrasts, however, allow that the dependence between species is taken into account (Harvey and Pagel 1991, Martins 1996). Reynolds and Székely (1997) applied such a method to study which factors may influence parental care in waders. They showed that the duration of care was related to sexual dimorphism: increases in the duration of caring time were associated with the decrease of relative body size in the given sex (Fig. 6). These results may be explained by sexual selection, because a decrease in relative body size may be due to a less intense sexual competition for mates. However, it is not known whether evolutionary changes in parental care induced a change in sexual dimorphism, or the effect of sexual selection over sexual dimorphism induced changes in parental care (Fig. 1. C). For a detailed discussion of the relationship between sexual selection and sexual dimorphism see Székely et al. (2000a).

Conclusions and proposed future research

Recent studies showed that the cooperation of parents during rearing their young is not harmonic, because each parent tries to maximise his/her own individual success. The diversity of parental care was recognised, and efforts were taken to explore factors that may influence parental care. However, our present knowledge is incomplete. Advancement is expected in at least three important areas.

Firstly, by developing parental care models not only the behaviour of other sex and other members of population should be considered but the quality and the state of individuals as well, because these influence largely the parental decisions. Therefore, development of state dependent game theoretical models is needed (Houston and McNamara 1999). Secondly, experimental studies are needed to explore the factors influencing the costs and benefits of parental care, because the theoretical models cannot be parameterised realistically without biological data. Furthermore, it is also necessary to test these models experimentally in the field or in the laboratory. Thirdly, it is expected that the comparative phylogenetic analyses of parental care will spread. However, to carry out phylogenetic analyses, we need phylogenetic hypotheses and knowledge of behaviour.

We know very little about the parental care strategies of most organisms living in Hungary. For example, of the relatively well represented birds, the parental care of only 5-10 species were studied with observations, and the number of species studied experimentally is even less.

What are the care patterns of fishes living in our rivers and lakes, and our amphibians and reptiles? Our current knowledge is very incomplete. It is likely that the study of these taxa (e.g. freshwater fishes, lizards) will give more interesting results than the currently dominating studies of birds and mammals.

Suggested reading

We suggest Clutton-Brock (1991) and the relevant chapters in books by Krebs and Davies (1993) and Alcock (1998). There are excellent chapters on parental care (Clutton-Brock and Godfray 1991) and mating systems (Davies 1991) in the third edition of *Behavioural Ecology: An Evolutionary Approach* edited by Krebs and Davies (1991). Furthermore, we suggest to read the reviews of Reynolds (1996) and Westneat and Sargent (1996). A review of parental care models and studies conducted on birds can be found in Székely et al. (1996). To those interested in paternity and paternal care, we suggest the book by Birkhead and Møller (1998) and the chapter of this book written by Wright (1998). A detailed description of comparative phylogenetic methods is found in Harvey and Pagel (1991), and we suggest the critical review of Martins (2000).

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Figure legends

Fig. 1. Theories of parental care and mating systems. A) The parental care determines the ratio of sexually active females and males (operational sex ratio, OSR) that, in turn, influences which mating system evolves (Emlen and Oring 1977). B) The OSR influences the mating opportunities and the parental care (Maynard Smith 1977). C) Bi-directional relationships. Mating strategies refer to the behavioural decisions of unmated individuals, whereas parental care strategies refer to the decisions of mated individuals. These strategies generate the distribution of mating patterns (e.g. monogamy, polygyny and polyandry), and the distribution of parental care patterns (frequency of biparental, male-only, female-only care, Székely et al. 2000b).

Fig. 2. Optimal parental care (c^*) in relation to the value of current ($B(c)$) and future ($F(c)$) offspring. If B and F are linear function of c , then based on the relative slopes of the two functions care is either maximal (Fig. A, $c^*=C$), or there is no care (Fig. B, $c^*=0$). If B and F are nonlinear functions of c , then even intermediate levels of care may be optimal (Fig. C). If the survival prospects of current offspring are higher than the average, then the slope of function B increases, therefore more care is expected (Fig. D, c^*_2 , Carlisle 1982).

Fig. 3. Straight lines describing the best response of males and females (Houston and Davies 1985). A) The best response of male to the effort of female. B) The best response of female to the effort of male. C–F) The possible positions of the two response functions. C) The line of male and the line of female cross, and the intersection is stable. The description of points 1–4 is in the text. D) The line of female lays above that of male, thus female-only care is the evolutionarily stable strategy (ESS). E) The line of male lays above that of female, thus male-only care is the ESS. F) The two lines cross, but the interception is not stable; it depends from the initial conditions whether male-only care or female-only care evolves.

Fig. 4. The possible ESSs in the parental care model of St. Peter's fish given the parameter plane determined by OSR (number of males / [number of males and females]) and the advantage of biparental care (P_2) against uniparental care (P_1 , Balshine-Earn and Earn 1998).

Fig. 5. The reconstructed phylogeny of parental care evolution in waders (Székely and Reynolds 1995). Male-only care (white), biparental care (black), female-only care (dotted) and equivocal (horizontal hatching).

Fig. 6. The relationship between evolutionary changes of parental care (contrasts), and evolutionary changes of sexual dimorphism (contrasts) in waders (Reynolds and Székely 1997). Sexual dimorphism was calculated from the wing length of males and females.

Fig. 1.

A



B



C

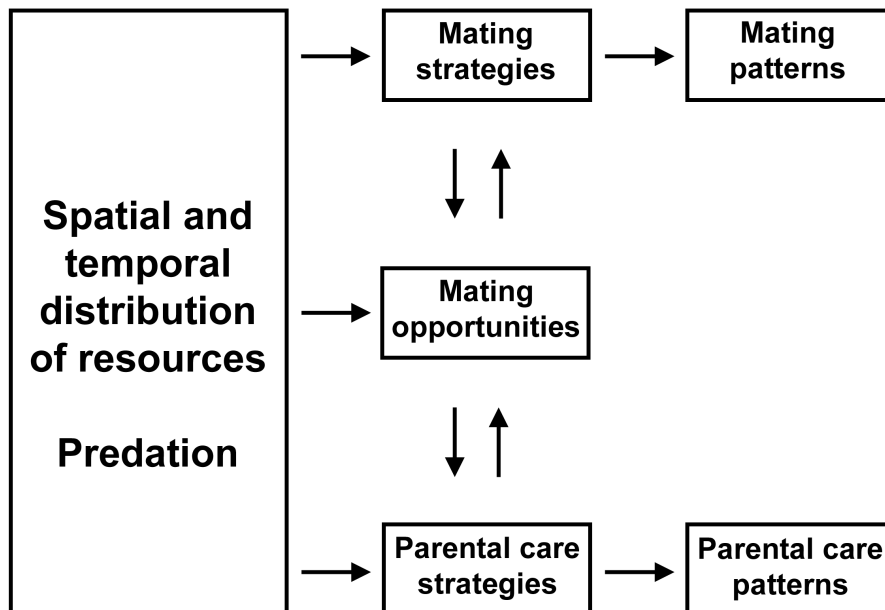


Fig. 2.

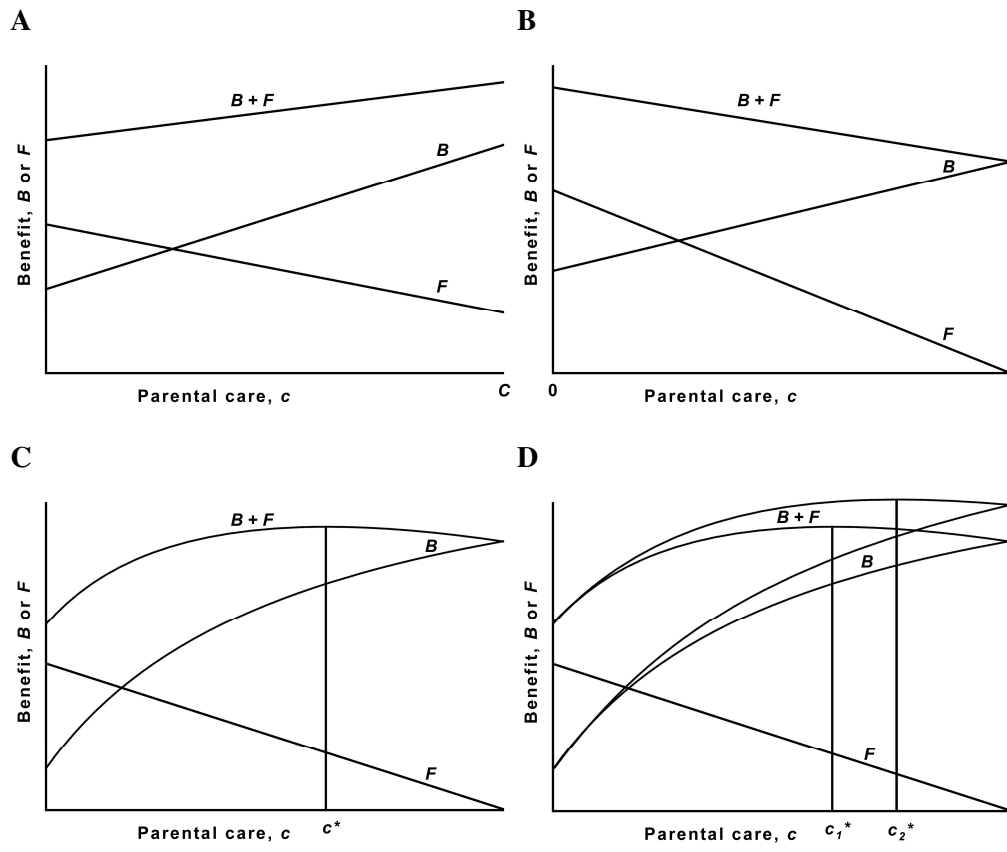


Fig. 3.

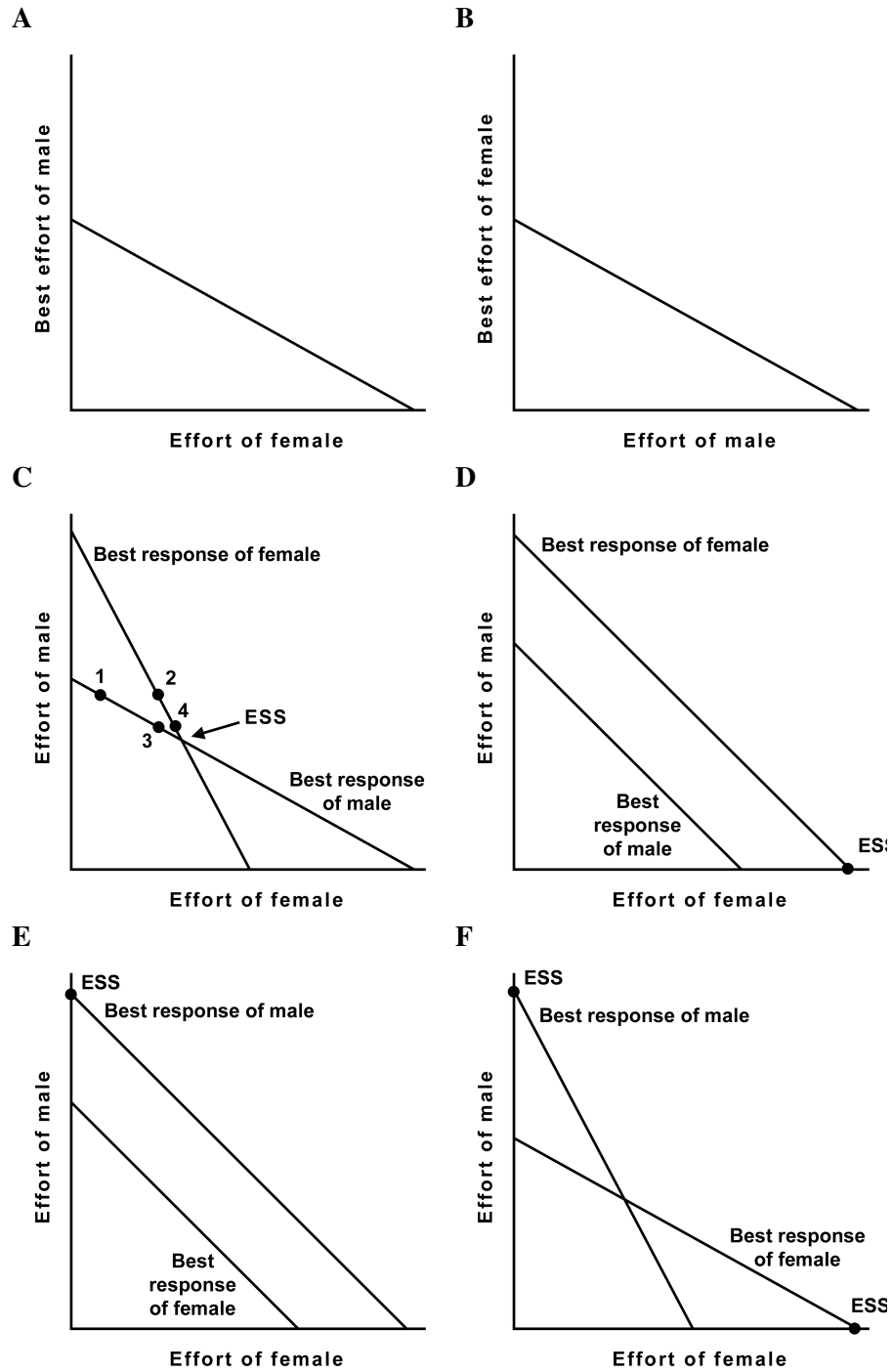


Fig. 4.

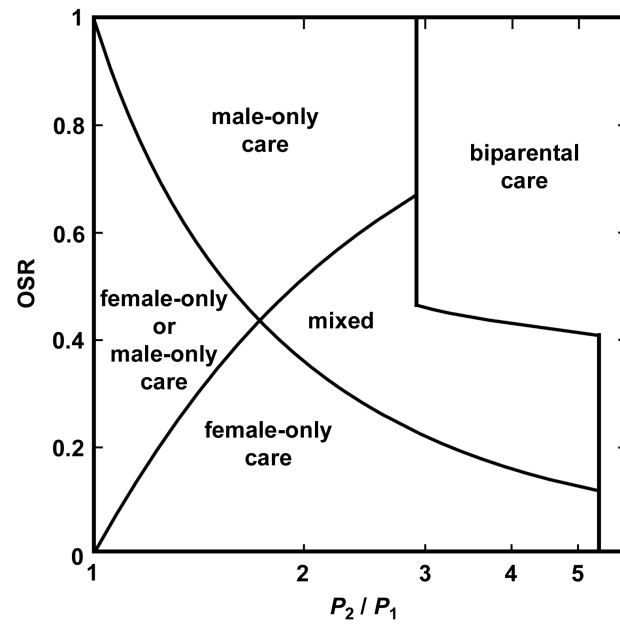


Fig. 5.

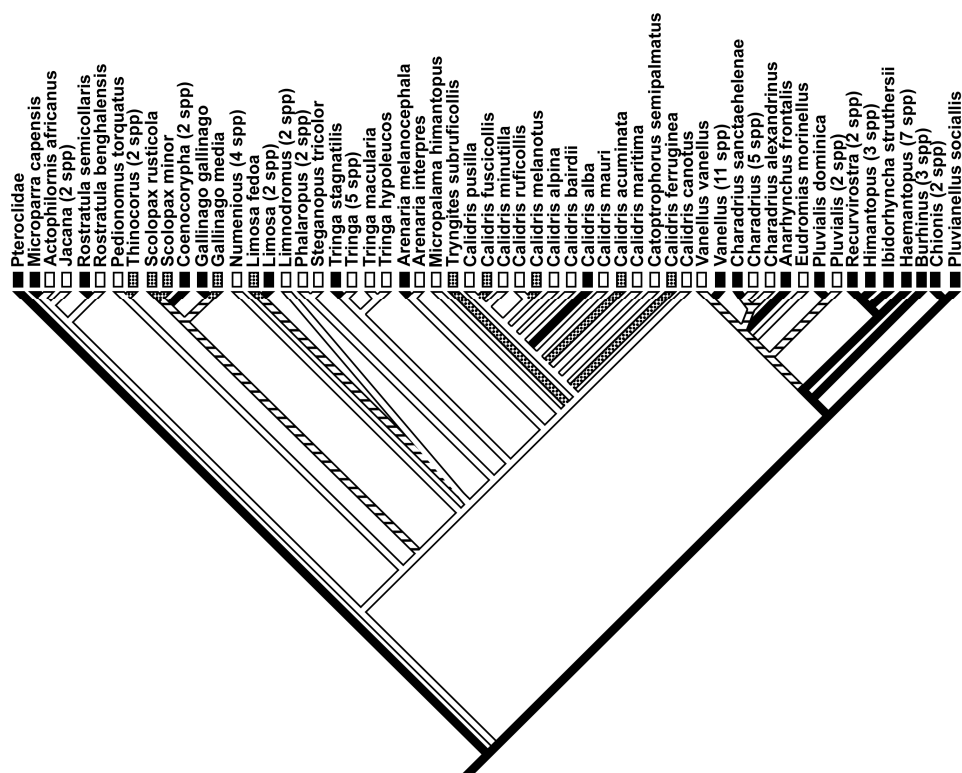
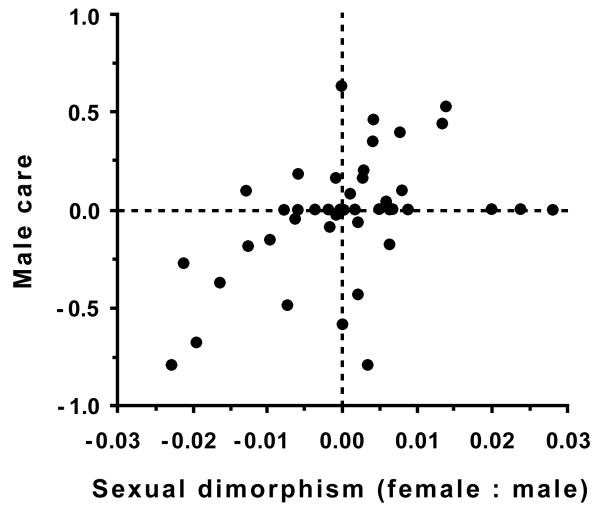
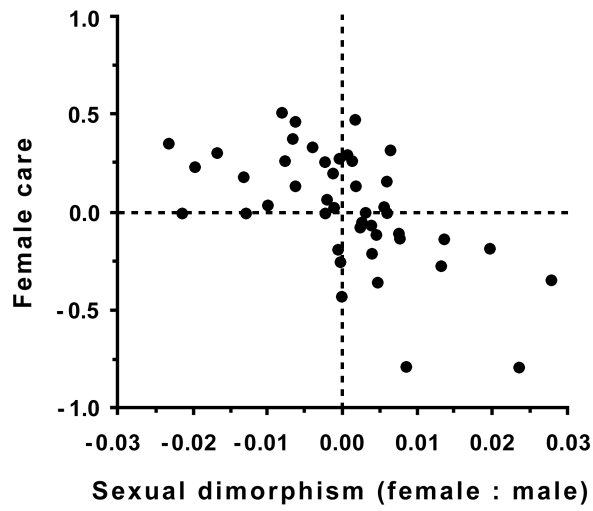


Fig. 6.

A



B



2.

**Using a transponder system to monitor
incubation routines of snowy plovers**

András Kosztolányi & Tamás Székely

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ABSTRACT. We investigated the incubation behavior of a ground-nesting shorebird, the Snowy Plover *Charadrius alexandrinus alexandrinus*, by developing a transponder system that recorded the identity of parents on their nest over 24 hours. The system consisted of a small chip glued on the tail of parent, an antenna that was buried under the nest and a recording device that was buried nearby. The transponder system was both accurate and reliable, since only 0.2% of records were false. The records of the transponder system were augmented by visual observations, and these data were analyzed by randomization tests. We found strong daily incubation routines: females incubated during the day, whereas males incubated mostly at night. Overall, the females spent more time incubating the nest (11.3 h (median) * day⁻¹) than the males (9.4 h * day⁻¹). We discuss several hypotheses for the observed daily incubation routines of sexes, and propose experimental studies to test these hypotheses.

Shorebirds *Charadrii* are ideal model organisms to investigate reproductive behavior, because they have a high variety of care patterns including incubation by both parents, only by the male and only by the female (reviewed by Erckmann 1983, Oring 1986, Reynolds and Székely 1997). Even in shorebirds with biparental care, there is substantial variation between the sexes. For example, males and females share incubation duties approximately equally in European Golden-Plover *Pluvialis apricaria*, Black Oystercatcher *Haematopus bachmani* and Purple Sandpiper *Calidris maritima* (Byrkjedal 1985, Purdy and Miller 1988, Pierce 1997), whereas most incubation is carried out by the female in Northern Lapwing *Vanellus vanellus* (Parish and Coulson 1998, Liker and Székely 1999).

We investigated the incubation routines of a ground-nesting precocial shorebird, the Snowy Plover *Charadrius alexandrinus alexandrinus*. Although brood-rearing behavior of Snowy Plovers has been extensively studied recently (Paton 1995, Fraga and Amat 1996, Székely and Cuthill 1999), their incubation behavior, especially nighttime incubation, is poorly understood. For example, previous investigations of incubation were carried out only in daytime (Purdue 1976, Nakazawa 1979, Paton 1995), and thus they do not provide unbiased information on the share of sexes.

The objective of our study was to investigate the daily routines of incubation by male and female Snowy Plovers both daytime and at night. To achieve this objective, we developed an automatic recording device (the ‘transponder system’). Although transponders are commonly applied in field avian studies to monitor survival (e.g. Becker and Wendeln 1997, Carver et al. 1999), our transponder system was developed and used to record incubation in a ground-nesting species.

Study site and methods

Fieldwork was carried out at Lake Tuzla (36° 43’ N, 35° 03’ E), southern Turkey. Approximately 1000 pairs of Snowy Plover bred in the saltmarsh around the lake (Székely and Cuthill 1999). Most of the vegetation was comprised of halophytic plants, such as *Artrochnemum fruticosum*, *Salicornia europaea* and *Sueda prostrata* (Uzun et al. 1995). The study was carried out in an area of approximately 52 ha on the north side of the lake over three years (15 April - 30 June 1997; 1 May - 20 June 1998; 15 April - 20 June 1999).

Both parents were caught on their nest by funnel traps, and banded with a metal band and an individual combination of color bands. The plumage of males and females is sufficiently dimorphic to allow the identification of the sexes. Behavioral records were collected only after the clutch was completed and the incubation had commenced. Only clutches of three eggs (modal clutch size, Székely et al. 1994) were investigated.

We used two methods to record the behavior of parents at their nest:

The transponder system. An automatic recording system was developed and used in 1997 to determine which parent incubated the eggs. First, we caught both parents on the same day or on subsequent days, and glued a 0.4 g plastic-coated passive chip (wedge-shaped TIRIS read-only transponder, Texas Instruments, US) on the tail feathers of each parent using Araldite glue (Evode Ltd., UK). Gluing the transponder lasted approximately for 15 minutes. Each transponder had a unique identification code. Each transponder weighed about 1% of adult body mass. Second, a circular antenna with a diameter of 9.5 cm was buried approximately 0.5 cm deep under the nest. To bury the antenna, we removed the complete nest including the eggs and the nest material, and once the antenna was in position than we put it back. The antenna was made of ceramic-coated wire and it was connected to a TIRIS Micro-reader. The reader was connected to a palmtop computer (PSION Organiser II), that controlled the reader and collected the data. The reader and the computer were enclosed in a box and buried approximately 0.5 m from the nest. Third, a car battery (12V), which powered both the reader and the palmtop computer, was buried approximately 5 m from the nest. The installation of the system took about 45 minutes. The installation was carried out early in the morning or late afternoon to minimize the impact of heat on the eggs. It is unlikely that the presence of the transponder system disturbed the parents, since all units of the system, including the cables, were hidden underground. The parents returned to the nest in a few minutes once the installation was complete.

Every 20 s the system read whether the male, the female, or neither parent was on the nest, and it stored the date, time and the identity of the parent if it was different from the previous record. If the system was unable to identify the transponder, then the record was stored as false. The system was able to record and store data for several weeks without interruption. Nevertheless, we checked it every day for proper operation. Each nest was recorded for at least 24 h. The parents lost the transponder by molting their tail feathers after the breeding season, as confirmed by four plovers that were fitted with a transponder in 1997 and recaptured in 1998.

Observations. The behavior of parents was also monitored from a blind at about 45 - 70 m from the nest using instantaneous sampling. Between 0600 h and 2100 h (local time, i.e. GMT + 3 hours) we recorded which parent (if any) incubated the nest every 30 s for two hours (in 1997), or every 20 s for two or three hours (in 1998 and 1999). All observations were carried out by AK.

To assess the reliability of the transponder system, data were collected simultaneously by both the transponder system and direct observations at five nests. During these observations the timing of the scans was synchronized with the system clock of the transponder system. No nest was abandoned due to capture or installment of the transponder system.

Statistical analyses

We considered each nest as the unit of the analyses (Table 1). If more than one nest was available for an individual (for instance, the plover laid a replacement nest or bred in several years) then we used the nest for which we had most records.

The reliability of the transponder system. We used two variables to assess the reliability of the transponder system: (i) total incubation time (%), that is the percentage of observations when the clutch was incubated by either parent; and (ii) incubation by the female (%), that is the percentage of total incubation time when the female incubated the clutch. If several visual observations were available for a parent, we used the mean of these observations.

Daily routine of incubation. Each day was divided into eight intervals ('interval' henceforward) of 3 hours each. Four variables were evaluated for these intervals: (i) total incubation time (%), (ii) incubation by the female (%), (iii) duration of male incubation, and (iv) duration of female incubation. For the first two variables, only the records that lasted for at least one hour in a given interval were included. The latter two variables were defined as the time that elapsed from the beginning of incubation by a given parent until the parent left the nest and the incubation was taken over by the other parent. Only those durations were included in the analyses in which both the beginning and the end of the incubation by a given parent were recorded. Each duration was assigned to the interval in which the incubation by that parent began. If several records were available for an individual in an interval, then the mean of these records for that interval was used. Incubation behavior was not different between years (two-way ANOVAs; total incubation time, year: $F_{2,74} = 1.404$, $P = 0.252$; time of day: $F_{3,74} = 9.068$, $P < 0.001$; interaction: $F_{6,74} = 1.388$, $P = 0.231$; incubation by the female, year: $F_{2,74} = 0.261$, $P = 0.771$; time of day: $F_{3,74} = 6.381$, $P = 0.001$; interaction: $F_{6,74} = 0.444$, $P = 0.847$).

Repeated observations of the same individual are not independent from each other. To control for this source of error, the daily activity was analyzed in two ways. (i) We used repeated-measures ANOVA in which time of day was the within-subject factor. Percentage variables were arcsine transformed, whereas the durations of incubation were $\log_{10}(x)$ transformed. In repeated-measures ANOVA ('ANOVA' henceforward) we used only the transponder data, because it requires data in all intervals for a given nest. For the duration of incubation by either the male or the female we had few data at night because change-overs were rare (see Results). Therefore, we kept the number of nests over four by excluding some intervals. (ii) We also investigated the daily activity using randomization tests (Manly 1997), in which data collected by either observations or the transponder system were included. Between-group sum of squares was used as test statistic and

the number of rearrangement was 10^5-1 . The randomization was carried out separately for each nest (stratified shuffling, Noreen 1989), i.e. only one record of a given nest was allocated to a given interval.

Statistical analyses were carried out using SPSS for Windows 8.0 (Norušis 1994). We provide the number of nests (N) and two-tailed probabilities. Medians (lower quartiles — upper quartiles) are given, unless otherwise stated.

Results

The reliability of the transponder system. The transponder system was both reliable and accurate in the field. The percentage of false readings was 0.2% of total recording time, and 96.0% of false readings lasted only for 20 seconds. The data collected simultaneously by an observer and the transponder system (dependent variable) were highly correlated and the slopes of linear regressions were not different from one (Pearson correlations, total incubation time: $r = 0.996$, $N = 5$, $P < 0.001$; incubation by the female: $r = 1.000$, $N = 5$, $P < 0.001$; t tests on the slopes, total incubation time: $b = 0.974$, $t_3 = 0.515$, $P = 0.642$; incubation by the female: $b = 1.008$, $t_3 = 0.585$, $P = 0.600$).

Daily routine of incubation. Eggs were incubated for 89.4% (86.8% — 94.0%) of the day by one or the other parent. Total incubation time was lowest between 0900 h and 1200 h (median: 79.7%), whereas it was highest between 1800 h and 2100 h (median: 98.0%, Fig. 1, upper). Total incubation time varied significantly over the day (ANOVA, $F_{7,35} = 6.190$, $N = 6$, $P < 0.001$; randomization, $N = 86$, $P < 0.001$).

Females provided 68.0% (13.5% — 90.9%) of total incubation (Fig. 1, lower). The share of incubation between the sexes varied significantly over the day (ANOVA, $F_{7,35} = 32.698$, $N = 6$, $P < 0.001$; randomization, $N = 86$, $P < 0.001$), since females spent more time incubating nests than males between 0600 h and 2100 h (Wilcoxon matched-pairs test, $Z = 5.495$, $N = 86$, $P < 0.001$, Fig. 1, lower), whereas nearly all incubation was performed by males between 2100 h and 0600 h (Wilcoxon matched-pairs test, $Z = 2.201$, $N = 6$, $P = 0.031$, Fig. 1, lower). Overall, females spent more time incubating the nest ($11.3 \text{ h} \cdot \text{day}^{-1}$ ($10.2 \text{ h} \cdot \text{day}^{-1}$ — $11.8 \text{ h} \cdot \text{day}^{-1}$)) than males ($9.4 \text{ h} \cdot \text{day}^{-1}$, ($9.1 \text{ h} \cdot \text{day}^{-1}$ — $9.8 \text{ h} \cdot \text{day}^{-1}$); Wilcoxon matched-pairs test, $Z = 2.201$, $N = 6$, $P = 0.031$).

Duration of incubation bouts. The duration of incubation bouts of males was 50.2 minutes (29.1 minutes — 188.7 minutes). Males incubated eggs throughout the night often without being relieved (Fig. 2, upper), whereas they incubated for short periods during the day (ANOVA, $F_{3,9} = 40.033$, $N = 4$, $P < 0.001$; randomization, $N = 32$, $P < 0.001$).

The duration of incubation bouts of females was 75.3 minutes (30.2 minutes — 231.0 minutes, Fig. 2, lower). We found no variation in female bouts between 0600 h and 1800 h (ANOVA, $F_{3,12} = 2.049$, $N = 5$, $P = 0.161$), although over the whole day there was a significant variation (randomization, $N = 18$, $P = 0.018$).

Discussion

The reliability of the transponder system. The transponder system was very reliable: the percentage of false readings was low and the correlation between the observations and the transponder data was high. This system is relatively cheap, since it costs USD 550 - 600 and one transponder is about USD 5. Therefore, we recommend this system to study incubation routines, particularly in ground-nesting birds (e.g. waterfowl, grouse and shorebirds).

We recommend to check the operation of the system on a daily basis, since we had a few cases when the system failed to record due to the corrosion of the antenna in the highly saline environment. False readings were rare, and they probably occurred when one parent was just about to settle on the eggs, or had just left, since the reading range of the antenna was small (10-20 cm), and the ability of the receiver to read the code of the transponder depended upon the angle between the antenna and the transponder.

Although the transponder system was precise, we identify three limitations. First, it is unable to distinguish between shading the eggs and true incubation. Shading of the eggs occurs at high ambient temperatures, for example in the Snowy Plover (Nakazawa 1979). Second, the system did not record when an untagged bird incubated the nest. For instance, in 1997 we tagged one male and one female at a nest, and later we also observed a second, untagged female incubating at this nest (this nest was not included in the current study). Incubation of a single nest by two females is very unusual in the Snowy Plover (Cramp and Simmons 1983). Third, humidity and a salty environment may damage the transponder system causing corrosion and electric shortcuts. To avoid these problems the antenna should be properly coated, and the system should be enclosed in watertight boxes. Watertight containers are also important to avoid flooding.

Daily routine of incubation. The percentage of time spent by one or the other parent on the eggs was high throughout the day, although we still detected a significant daily variation. The highest percentage of incubation occurred at night, in early morning and at midday. These results agree with previous observations that incubation is most intensive when the ambient temperature is extremely cold or hot (Purdue 1976, Nakazawa 1979).

Our study overcomes two limitations of previous studies in Snowy Plovers (Purdue 1976, Nakazawa 1979, Paton 1995). First, in these studies the behavior of parents was investigated only during the daylight period; thus it was not known which sex (if any) incubated at night. Full 24 hour records are important, for example to reveal the contribution of each sex to total care provisioning. Second, some of the previous studies did not use appropriate statistical tests. For example, Purdue (1976) assumed that each of his observations was independent. Clearly, this was not the case, and appropriate statistical tests such as repeated-measures ANOVA and randomization tests are required to avoid pseudoreplication.

In several plovers (e.g. Wilson's Plover *Charadrius wilsonia*, Killdeer *Charadrius vociferus*, Semipalmated Plover *Charadrius semipalmatus* and Snowy Plover), the female incubates mostly during the day, whereas the male incubates at night (Thibault and McNeil 1995, Warnock and Oring 1996, Blanken and Nol 1998, this study). We propose four reasons for the different daily routines of males and females. First, females may forage at night to recover their energy deficit, especially shortly after egg-laying (Staine and Burger 1994). Therefore, males (that are not exhausted by egg-laying) are able to spend the night on the nest, whereas the females may need to carry on foraging. However, this hypothesis is unlikely to explain incubation routines in our study, since in our population the plovers rarely feed at night (Kosztolányi and Székely pers. obs). Second, the male may have to defend the territory during daytime, which restricts his ability to help his mate to incubate. However, Snowy Plovers do not maintain territories around their nest in our study site (Kosztolányi and Székely pers. obs). Third, male Snowy Plovers have black breast-bands and head-stripes, and cinnamon crowns, whereas the females are pale brown. Therefore, the more colorful male may be more conspicuous to visually searching predators than the dull female, and thus males may be more likely to give away the location of nest during daytime. Fourth, males and females may have different abilities to detect predators approaching the nest. Wilson's Plovers sit motionless on the nest during daytime, but they scan all directions to detect predators at night (Thibault and McNeil 1995). If males are better at detecting the predators at night than females, for instance because they may have better eyesight, then they may be able to leave the nest earlier than females if a predator approaches. We conclude that the first two explanations are unlikely in our study site, whereas the latter two warrant further investigation.

Incubation bouts of males were long at night, whereas females had much shorter bouts. These observations suggest that males are more persistent incubators than females. Females presumably have depleted energy reserves due to the egg-laying (e.g. Thibault and McNeil 1995), and thus they may not be able to undertake the whole daylight incubation without interruption.

In conclusion, we recommend the transponder system to record incubation behavior in ground-nesting birds. Our experiences were positive since the

transponder system was both accurate and reliable. We also showed that male and female Snowy Plovers have different daily incubation routines. Such a difference may emerge if the costs or the benefits of incubation vary over the day. Future observations on the daily routines, and experimental manipulations of males and females will be important to determine how these costs and benefits influence incubation behavior, and whether the male or the female drive the observed incubation patterns.

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Table 1. Laying date and incubation stage of investigated nests ($N = 22$ in 1997, 24 in 1998, 40 in 1999). Laying date is the number of days since 1 January, and incubation stage is the number of days for which the clutch had been incubated for at the time of behavioral records.

Year	Mean \pm SE laying date (range)	Mean \pm SE incubation stage (range)
1997	138.4 \pm 3.3 (116 - 175)	14.3 \pm 1.1 (1 - 23)
1998	140.9 \pm 2.7 (115 - 162)	9.8 \pm 0.9 (4 - 19)
1999	136.4 \pm 2.6 (105 - 164)	8.9 \pm 0.7 (3 - 21)

Figure legends

FIG. 1. (upper) Total incubation time (%), and (lower) incubation by the female (%) over the day ($N = 86$ nests, 1098.8 hours in total). Medians, interquartile ranges (boxes), lowest and highest observations (whiskers) within the range of $LQ - 1.5*(UQ - LQ)$ and $UQ + 1.5*(UQ - LQ)$, and outliers (squares) are given, where LQ is the lower quartile and UQ is the upper quartile.

FIG. 2. (upper) Duration of incubation bouts by males ($N = 32$ nests, 908.2 hours in total), and (lower) by females ($N = 18$ nests, 840.2 hours in total) over the day. See Figure 1 for legend. Incubation bouts are given for the time period in which they started.

Fig. 1.

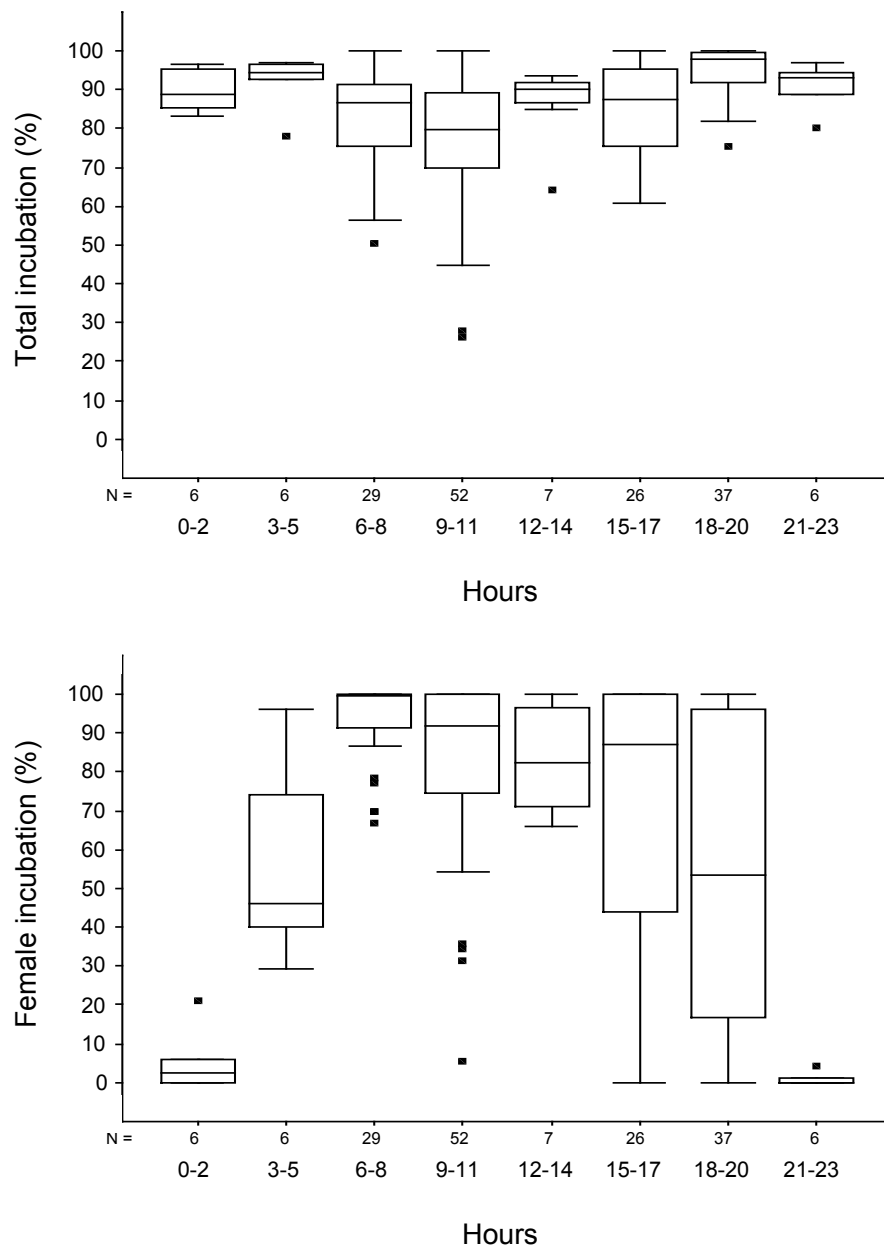
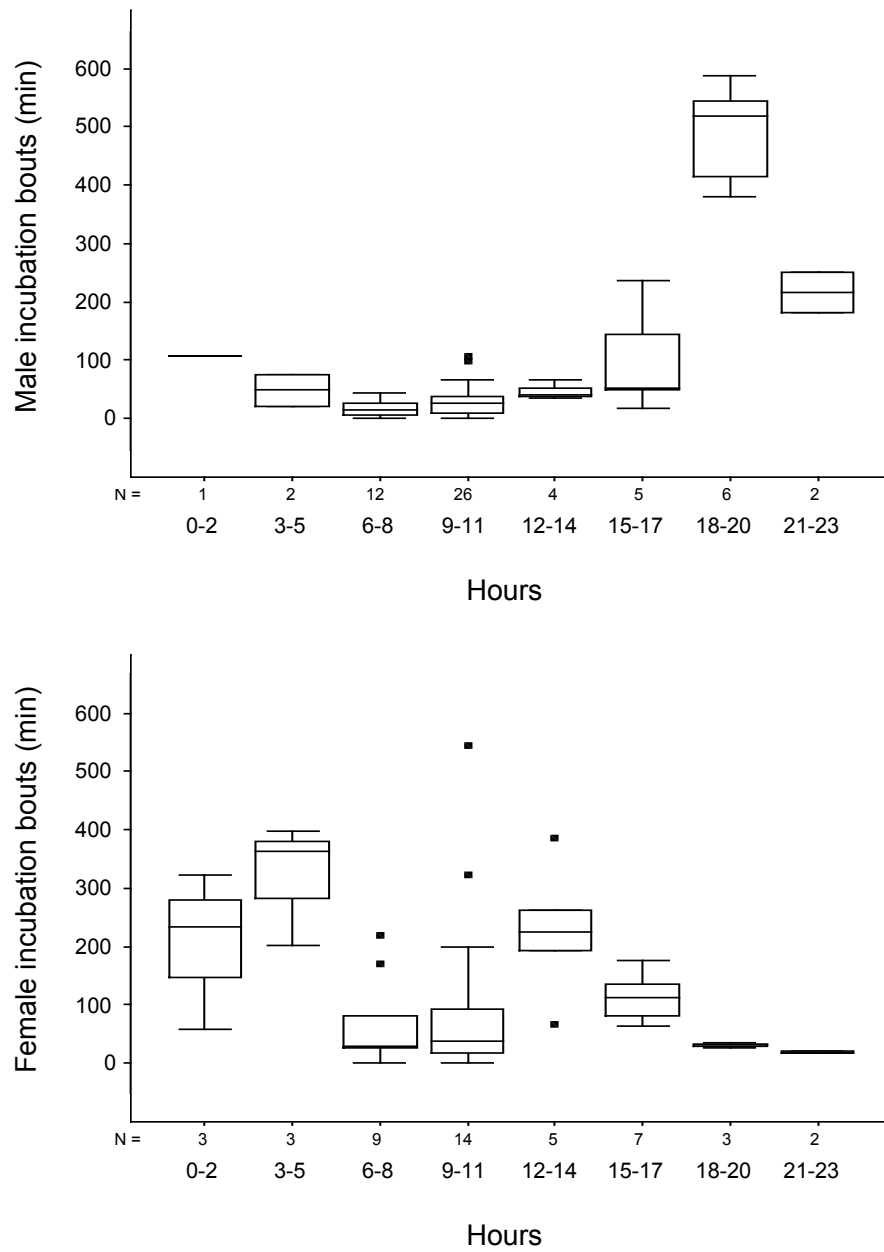


Fig. 2.



3.

**Daily changes in body mass of incubating
Kentish plovers**

István Szentirmai, András Kosztolányi & Tamás Székely

Ornis Hungarica 11: 27–32, 2001

We investigated the daily body mass changes in incubating female Kentish plovers *Charadrius alexandrinus*. We found that the body mass of females decreased over the day. The change in body mass was significant both from morning to midday (median decrease: 3.36%), and from morning to afternoon (8.40%). We suggest two reasons for this decrease: depletion of fat reserves and the evaporation of water from body tissues. These changes may either indicate a physiological cost of incubation, or they may be the result of a strategic body mass regulation.

Introduction

One of the key issues in behavioural ecology is how animals allocate time and energy to various activities (Cuthill & Houston 1997). Since resources are often limited, there must be trade-offs between various life-history components. For example, parent birds may enhance their current reproductive value by spending time and energy on incubating their clutch and raising their young, although these behaviours may reduce their residual reproductive value (Roff 1992, Kosztolányi & Székely 2002a). Such trade-offs are often interpreted as acting directly through the depletion of body reserves, i.e. it may indicate a cost of reproduction (Jones 1988, Kacelnik & Cuthill 1990). For example, low body reserves may reduce the chance of initiating a new clutch either in the same breeding season or in future years, or they may reduce the chances of parent's survival until future breeding seasons (Hemborg 1999).

Mass loss during breeding is often interpreted as an indicator of physiological stress. For example, a significant mass loss during incubation has been detected in several Passerines (Moreno 1989, Halpern et al. 1997). Furthermore, a positive relationship was observed between mass loss of females and their reproductive effort, whereas the females' ability to allocate energy to self-maintenance decreased with mass loss (Merilä & Wiggins 1997).

Two types of body mass variation have been reported during incubation. Firstly, the mass of the incubating parent decreased in those species in which incubation was carried out by a single parent and/or nest attentiveness was very high (Moreno 1989, Hegyi & Sasvári 1998). This change may be due to the fact that the incubation metabolic rate (IMR) is often elevated above the metabolic rate of non-incubating birds, e.g. by 19-50 % in Passerines (Williams 1996). Secondly, body mass did not show any trend over the course of incubation in those species in which both parents incubated the clutch and/or in which the nest was attended for a low percentage of time (Moreno 1989, Hegyi & Sasvári 1998).

The reproductive stress hypothesis, which argues that the mass loss of breeding birds is due to the increased energetic expenditure, has been frequently criticised. For example, mass loss may simply be due to degeneration of the reproductive organs (Ricklefs & Hessel 1984), or the loss of body mass may be an adaptive adjustment to reduce energetic cost of flight during brood rearing when the demands of the offspring increases (Norberg 1981). Finally, low body mass reduces wing loading and enhances the take-off ability and flying performance, and thus reduces the risk of predation (Witter & Cuthill 1993).

Although shorebirds *Charadrii* have an immense annual variation in their body mass due to migratory fattening (Piersma 1994), only few body mass

changes are documented during the breeding season. Nevertheless, these studies would be particularly important in shorebirds, since it has often been hypothesised that the changes in their body mass (and body condition) should influence their mating and parental behaviours (Ashkenazie & Safriel 1979, Erckmann 1983). Also, many shorebirds breed on the ground, and thus the cost of keeping the eggs within the required temperature range, e.g. on the frozen tundra (Piersma & Morrison 1994) or on desert sand, may have significant consequences on the body mass of incubating parent(s). In line with this argument the body mass of several subarctic shorebirds tended to decrease during reproduction (Soloviev & Tomkovich 1997), possibly due to their elevated metabolism.

The objective of our study was to investigate the daily changes in body mass of female Kentish plovers *Charadrius alexandrinus*. Kentish plovers are small ground-nesting shorebirds. Their incubation period is about 25 days and their chicks are precocial. Both the male and the female incubate the clutch (Kosztolányi & Székely 2002b), although shortly after hatching of the eggs one parent commonly deserts the brood (Paton 1995, Székely & Cuthill 2000). Males typically incubate at night, whereas females incubate mostly during the daylight period (Kosztolányi & Székely 2002b).

Study area and methods

Field work was carried out in May 1999 in Southern Turkey, near the village of Tuzla (36°42'N 35°03'E). The study site was a salt marsh between Lake Tuzla on the south and arable land on the north. The size of the breeding population of Kentish plover was about 1000 pairs (Székely et al. 1999).

Females were caught on their nest by a funnel-trap, and ringed with a metal ring and an individual combination of colour rings. Each female was captured three times: in the morning (06.00 h – 09.00 h, local summer time, i.e. GMT + 3 hours), at midday (11.00 h – 14.00 h) and in the afternoon (16.00 h – 19.00 h). At every capture their body mass was measured (± 0.1 g). Captures of the same female were carried out on different days. We randomised the sequence of captures for each female to eliminate carry-over effect. The interval between first and second captures was 1.11 ± 0.20 days (mean \pm SE), and between the second and third captures was 2.00 ± 0.53 days. Only nests with three eggs (modal clutch size, Székely et al. 1994), and those incubated for more than three days were investigated. Further details of field methods are given elsewhere (Székely et al. 1999, Székely & Cuthill 2000, Kosztolányi & Székely 2002b).

The distribution of body mass was not normal, thus we used non-parametric tests such as Friedman two-way ANOVA (factor: time of the day, block: individuals). Comparisons between groups were conducted using Wilcoxon

matched-pairs signed-rank tests. In the latter analyses we corrected the significance level for multiple comparisons by sequential Bonferroni adjustment (Chandler 1995). We used SPSS for Windows for statistical analysis. Values are given as median (lower quartile — upper quartile), and we provide the exact two-tailed probabilities. In all analyses the sample size was nine females.

Results

Body mass of females decreased during the day from 41.8 g (41.0 g — 43.5 g) in the morning to 40.3 g (39.8 g — 42.7 g) at midday, and 39.8 g (37.9 g — 40.4 g) in the afternoon (Fig. 1.). Thus the body mass of females decreased by 3.36% (2.81% — 4.98%) from morning to midday, by 3.72% (2.11% — 6.77%) from midday to afternoon, and by 8.40% (1.69% — 10.56%) from morning to afternoon. We estimated that females lost about 0.33 g / hour (0.07 g / hour – 0.45 g / hour) of their body mass from morning till afternoon.

The mass change between morning, midday and afternoon was highly significant (Friedman test, $\chi^2 = 9.314$, $df = 2$, $P = 0.007$). The difference in body mass was also significant both between morning and midday (Wilcoxon matched-paired signed-ranks tests, $Z = 2.549$, $P = 0.008$), and morning and afternoon ($Z = 2.310$, $P = 0.020$), whereas the mass change was not significantly different between midday and afternoon ($Z = 0.980$, $P = 0.383$).

Discussion

Our results show that incubating female Kentish plovers lose mass during the day. This result was unexpected, since females often interrupt their incubation by either spending a few minutes in the vicinity of nest and then resuming incubation, or being relieved by their mate for a variable period of time (Kosztolányi & Székely 2002b). In these recess times the females typically forage. Thus the total loss in body mass would have been larger if the females were to incubate constantly during the investigated daytime periods.

We suggest two ways for the observed loss in body mass: depletion of stored body fat and evaporation of water. Depletion of fat stores can be the result of the increased energetic demands of incubation or starvation. For example, it is probably costly to maintain the egg-temperature within the range in which the embryonic development is normal (i.e. between 30 to 40 °C, Purdue 1976). Female Kentish plovers relieve their incubating mate at dawn (Kosztolányi & Székely 2002b), when the ambient temperature is low. At this time of the day an increased metabolic rate may be required to keep the egg temperatures in the optimal range.

At midday, when the ambient temperature is high, the parent has to cool the eggs. Thus, at midday the parents often shade the eggs and they may themselves lose a considerable amount of water by evaporation (Hinsley & Ferns 1994). Also, cooling the eggs may elevate the energy expenditure of the parents, for instance an increase of 1.3 BMR was shown in sandgrouse (Hinsley & Ferns 1994). So both cooling and keeping the eggs warm may be costly for the incubating parent, and thus they may result in depletion of fat reserves. The significant decrease in body mass between morning and midday suggests that heating the eggs may be more demanding than cooling in the Kentish plover.

While the parent is restricted to sitting on its nest, it cannot replenish the lost reserves by feeding. For example, one reason why female Kentish plovers stop incubating in the evening may be that they have to replenish their body reserves (Purdue 1976, Paton 1995). The other possibility is that nighttime incubation is more demanding than incubation during daytime, and thus if females are exhausted by egg laying (Monaghan *et al.* 1998) then the males are in a better position to carry out nighttime incubation. Future studies, preferably experimental manipulations, are required to identify how the various costs and benefits of incubation vary over the day.

Although we have limited information on the other potential explanations for the observed daily mass loss (such as the degeneration of reproductive organs and strategic body mass regulation), we make the following inferences. Firstly, it is unlikely that the loss of body mass was due to degeneration of reproductive organs (Ricklefs & Hussel 1984), since female body mass changed in a short, i.e. daily basis. Secondly, the strategic adjustment of body mass seems more plausible (Moreno 1989, Witter & Cuthill 1993, Thomas 2000), and we encourage researchers to consider the explanation that reducing body mass may be advantageous for requiring low cost of self-maintenance and/or for reducing the risk of predation. Nevertheless, we do not see any apparent reason why such mass loss would be adaptive only between morning and midday in the Kentish plover.

In conclusion, our results show that the body mass of female plovers decreases during the day. This decrease may indicate a cost of incubation in terms of depletion of fat reserves and evaporation of water, although we cannot rule out the alternative explanation that body mass regulation is strategic.

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Összefoglalás

Széki lilék napi tömegváltozása a kotlás alatt

Széki lile tojók napi tömegváltozását vizsgáltuk a dél-törökországi Tuzla-tónál 1999 májusában. Az általunk vizsgált kilenc tojó mindegyikét három alkalommal fogtuk be és lemértük a tömegüket: reggel (06.00-09.00 h), délben (11.00-14.00 h) és délután (16.00-19.00 h). Mivel a befogások nem azonos napon történtek, ezek sorrendjét randomizáltuk.

Kimutattuk, hogy a tojó széki lilék tömege szignifikánsan csökken a nap során a kotlási periódus alatt. A madarak tömege 41.8 g (medián) volt reggel, 40.3 g délben és 39.8 g délután. Mind a reggeltől délig, mind a reggeltől délutánig történő tömegcsökkenés szignifikáns volt, míg déltől délutánig a madarak tömege nem változott szignifikánsan.

A vizsgálatunkban megfigyelt testtömeg csökkenésnek két okát feltételezzük. Az egyik a szülői zsírtartalékok leépülése, a másik a párologtatás során bekövetkező vízvesztés. A zsírtartalékok leépülése feltehetően a kotlás megnövekedett energetikai igényeinek a következménye, ami különösen nagymértékű lehet a reggeli órákban, amikor a tojásokat melegíteni kell az embriók normális fejlődéséhez (szignifikáns tömegcsökkenés reggeltől délig). A tojók vízvesztését a tojások evaporatív hűtése okozhatja a meleg déli órákban. Ráadásul amíg a szülők kotlanak a fészken csak korlátozott mértékben tudják táplálkozással és ivással pótolni a készleteiket. A tömegcsökkenés tehát utalhat a kotlás költségeire, ugyanakkor nem zárhatjuk ki azt sem, hogy stratégiai szabályzás eredménye. Ennek tisztázására további vizsgálatok szükségesek.

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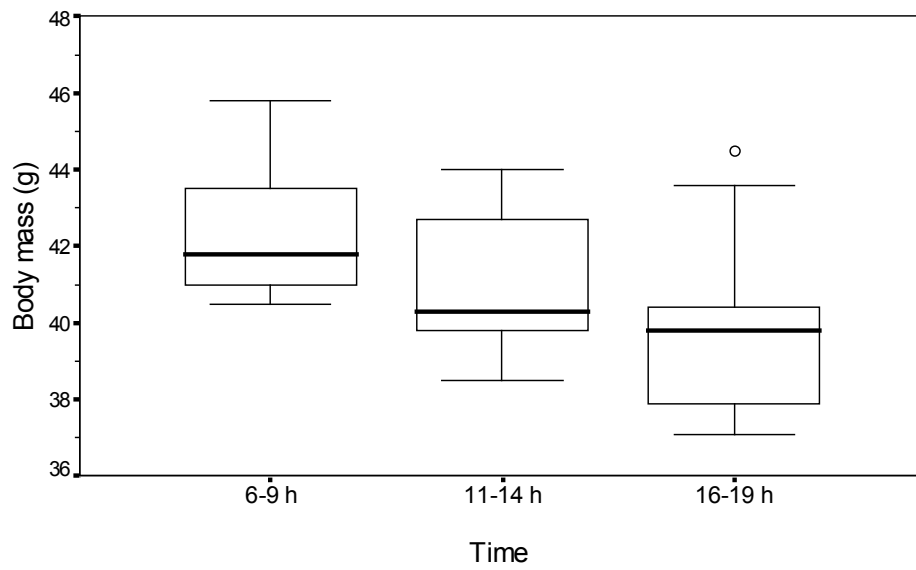
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Figure legends

Fig.1. Body mass of incubating female Kentish plovers over the day ($n = 9$ females in all three periods). The thick horizontal line indicates the median; the bottom and the top of the box are lower (Q_1) and upper quartiles (Q_3), respectively. The whiskers indicate the lowest and highest observation, within the range defined by $Q_1 - 1.5*(Q_3 - Q_1)$ and $Q_3 + 1.5*(Q_3 - Q_1)$. An outlier is indicated by a circle.

Fig. 1.



4.

**Why do both parents incubate in the Kentish
plover?**

András Kosztolányi, Tamás Székely & Innes C. Cuthill

Ethology (provisionally accepted)

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.

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, since 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 et al. 1999; Székely & Cuthill 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. It has been proposed that 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 parents than in unsupplemented ones.

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 approximately 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) days ($n = 139$ nests, A. Kosztolányi & T. Székely unpublished 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 four days 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 approximately 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 x 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 $103 \text{ kJ} \cdot \text{day}^{-1}$ (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 hours starting between 0700 h and 1800 h (local time, i.e. GMT + 3 h). The samples started 15 min after the observer (AK) arrived to the observation point. There is a strong diel pattern in incubation behaviour (Kosztolányi & Székely 2002), therefore the timing of behavioural records was matched on Day 2 and Day 4 ($\pm 1 \text{ h}$) for each nest.

The experiment was carried out in two years; between 1 May - 20 June in 1998 (30 nests) and between 15 April - 20 June 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 days at each nest (Days 1-2: observations for two hours on each day; Day 3: manipulation; Days 4-5: observations for two hours on each day). Thus removal and food supplementation lasted for two days, and 5 x 30 mealworms were provided at each supplemented nest. We found no difference between the two protocols, since 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 January 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 days, $F_{4,60} = 0.017$, $p = 0.99$; incubation stage: range 2 - 17 days, $F_{4,60} = 0.90$, $p = 0.47$; clutch volume: range: 20.8 - 27.4 cm^3 , $F_{4,60} = 1.29$, $p = 0.29$).

Ethical Note

The experiment involved temporary removal of the male or female of incubating pairs, so there are several ethical issues to consider. First, we note that the removal lasted on average only 1.6 (range 0.9 - 2.3) days, 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) * 2.5 m (L) * 0.8 m (H) purpose-built cages. A maximum of five plovers was housed in a cage at the same time. *Ad lib.* 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 due to time constraints, although 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 experimental pairs hatched their eggs out of 65, and this is not different from the hatching success of unmanipulated nests (at least 17 nests hatched out of 66, $\chi^2_1 = 0.20$, $p = 0.66$). Thus, our experimental design and the choice of sample size was a compromise between minimising 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 % of time when the clutch was incubated by either parent, (ii) male incubation was the % of time when the nest was incubated by the male, and (iii) female incubation was the % 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). First, in the analyses of total incubation, four contrasts were used in which the control nests were contrasted against all other nests; i.e. for the treatments (i) to (v) specified earlier, the contrast weights are 1, 1, 1, 1, -4 (see Norusis 1988). Second, the effect of removal was investigated by comparing female-only and male-only nests with control ones (1, 0, 1, 0, -2). Third, 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, 0). Fourth, we looked for the effect of interaction between removal and food supplementation by contrast weights 1, -1, -1, 1, 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, 1; where the contrasts are given for single-parent, single-parent + food and control nests). Second, 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, 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). Diurnal changes in body mass of parents, however, 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 used SPSS for Windows 8.0 in statistical analyses. Mean \pm SE and two-tailed probabilities are given.

Results

Uniparental nests were incubated for a lower percentage of time (46.9 ± 4.5 %, $n = 52$) than biparental controls (69.1 ± 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 ± 4.0 %, $n = 42$, control = 74.8 ± 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, 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: $t_{36} = 3.59$, $p = 0.001$; 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 ± 3.5 %) than males (17.5 ± 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: $t_{15} = 0.79$, $p = 0.44$).

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 result 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 days (males) or 9 days (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 out of 52 unassisted parents did not incubate during the behavioural sample, whereas in Lessells' study 8 out of 29 unassisted parents (2 males and 6 females) deserted their nest. Second, 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 renesting period after experimentally raised parental effort as it has been shown in black swans (Brugger & Taborsky 1994).

The demand for biparental care, however, is not the only reason for the occurrence of biparental care, because the parents may also stay with their mate and offspring if the payoff from desertion is low (reviewed by Clutton-Brock 1991; Székely et al. 1996, Ligon 1999, Bennett & Owens 2002), or if their mate prevents them for 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 *Chen rossii* (Gloutney et al. 1999). There may be three reasons for this. First, both in our study and in Gloutney et al.'s 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. Second, 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 out 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). Third, 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, since 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.

Acknowledgements

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Figure Legends

Fig. 1: Total incubation (mean \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: $F_{4,49} = 1.68$, $p = 0.17$).

Fig. 2: Male incubation (mean \pm 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: $F_{2,32} = 8.54$, $p = 0.001$).

Fig. 3: Female incubation (mean \pm 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).

Fig. 4: Body mass (mean \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: $F_{2,15} = 0.41$, $p = 0.67$).

Fig. 1.

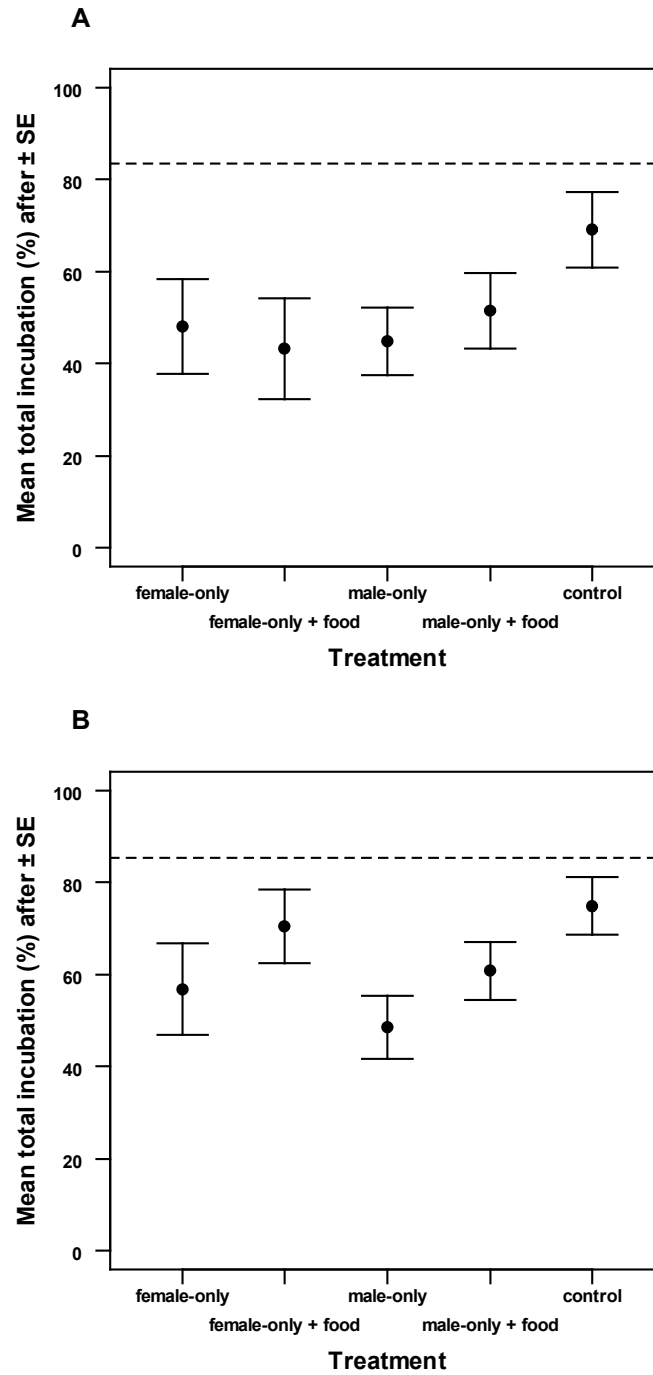


Fig. 2.

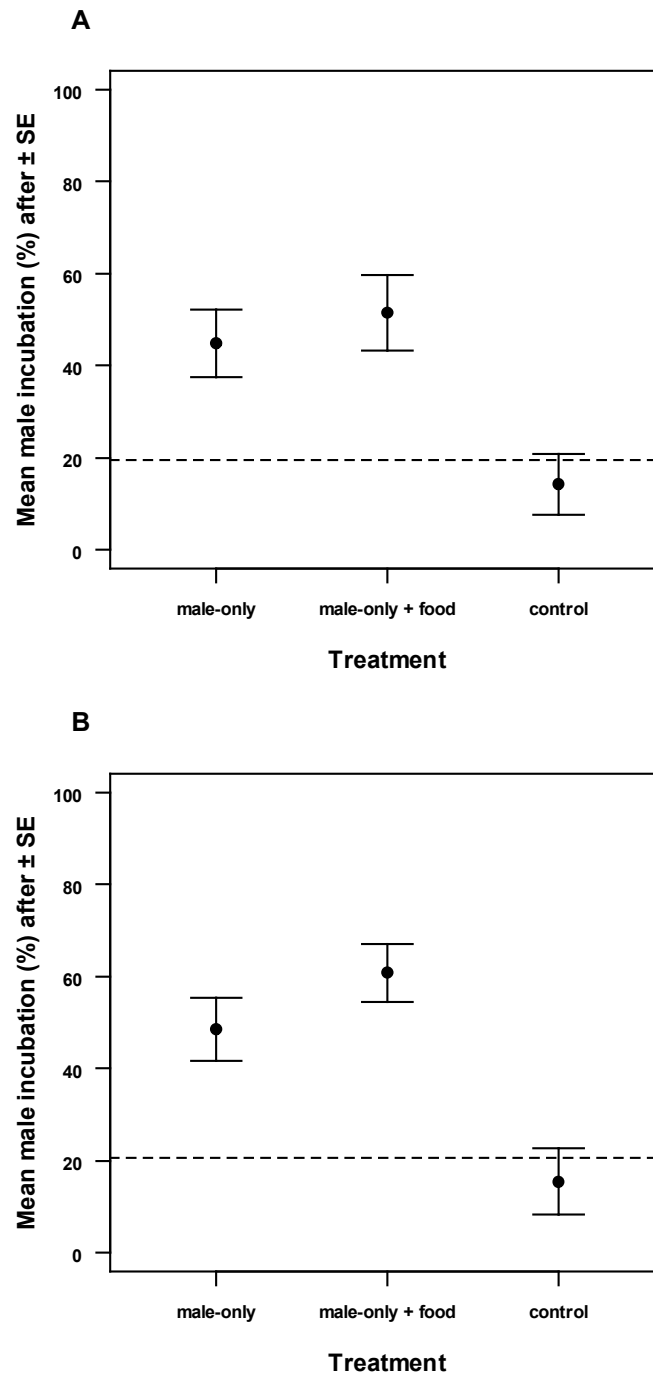


Fig. 3.

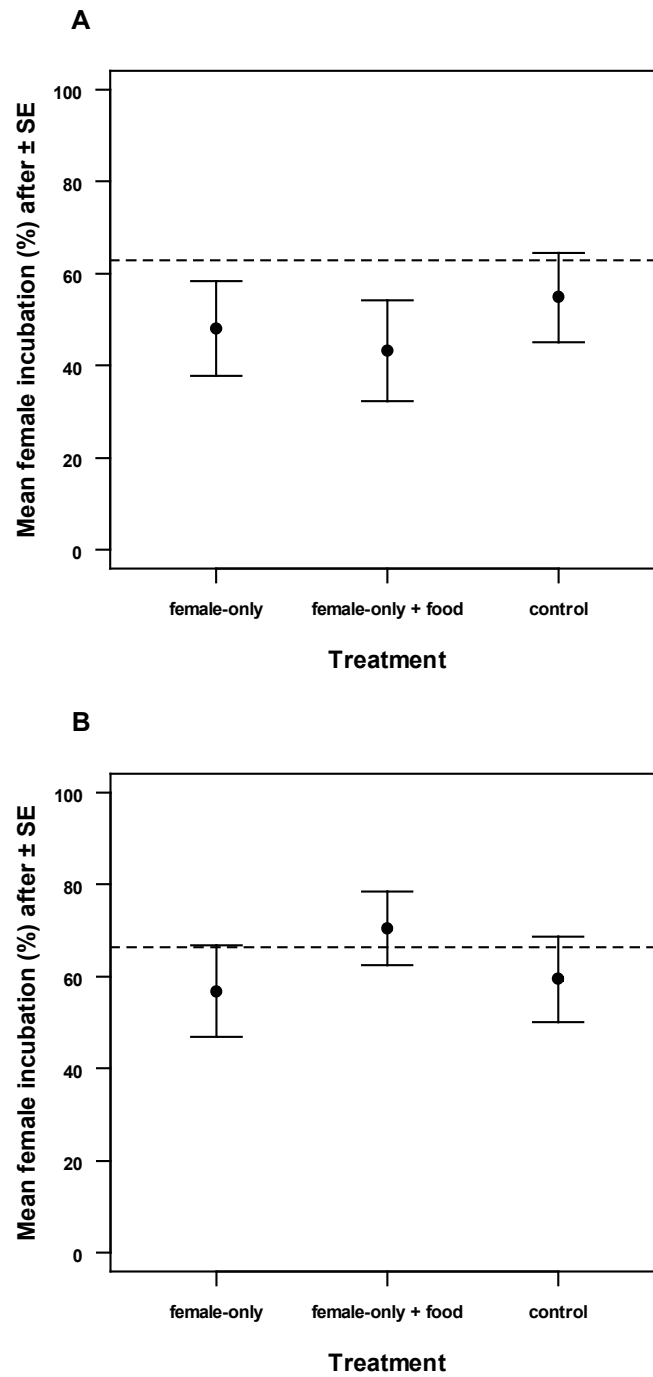
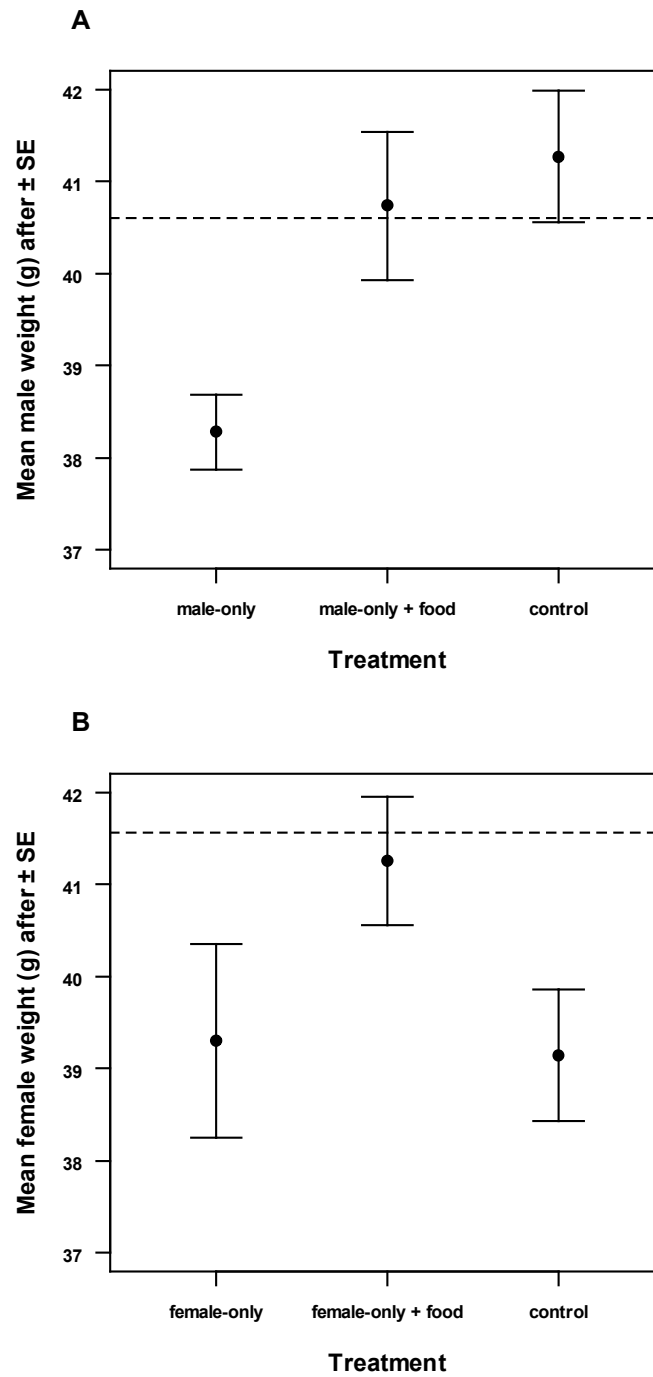


Fig. 4.



5.

The influence of habitat on brood-rearing behaviour in Kentish plover

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manuscript in preparation

Abstract

Where should the parents raise their young? Parents with well-developed and mobile young may leave the nest and rear their young in a habitat that is safe from predators and/or provides resources for the developing offspring. However, if the costs and benefits of rearing the brood in a given environment changes over time, either because the habitat itself is changing or the needs of the offspring change as they develop, then the parents are expected to move with their young between habitats. We investigated the brood-rearing behaviour of a precocial shorebird, the Kentish plover *Charadrius alexandrinus*. This species has a variable pattern of brood care, since one parent often (but not always) deserts the offspring. Kentish plovers reared their broods in two habitats in Southern Turkey: in the saltmarsh and on the lakeshore. We found that broods spent more time on the shore as the season proceeded. This shift is consistent with our observations that the food intakes of chicks and parents were higher on the lakeshore than in the saltmarsh, particularly late in the season when the saltmarsh dried out. As a result of brood movements, the density of plovers increased on the shore and the parents fought more on the lakeshore than in the saltmarsh probably to defend the brood's feeding territory against neighbouring broods. In addition, the duration of biparental care of broods lasted for longer on the lakeshore than in the saltmarsh. Taken together, the Kentish plover is one of the few species in which the ecology of brood-rearing habitat influences the brood-rearing behaviour and the patterns of parental care.

Introduction

The requirements of young are often different from their parents: they are more vulnerable to predators and they need concentrated resources to develop rapidly. If the young are precocial, i.e. well-developed at birth, then the parents may take their young to various habitats during parental care. For example, shorebirds and ducks often lead their chicks after hatching from the nest site to habitats where the young can feed (Walters 1984, Sedinger 1992).

Movement and habitat change may be beneficial for the young in a number of ways. Young ungulates and macropods living in open habitats have young that follow their mothers because young hiding in sparse vegetation would suffer higher predation (Fisher et al. 2002). Also, mammals with mobile offspring are less vulnerable to infanticide by conspecific females and therefore do not defend a territory (Wolff & Peterson 1998). emperor geese *Chen canagica* nest in an area that contains a high density of plants with good nutritional content. Nevertheless, the parents move with their goslings to a less profitable habitat after hatching to avoid predation or competition (Laing & Raveling 1993). Competition is the likely reason also for leading chicks away from nesting site in sandwich terns *Sterna sandvicensis*. Leading young away from the colony reduces kleptoparasitism by gulls and so results in improved condition and growth rate of chicks and a shorter pre fledging period (Stienen & Brenninkmeijer 1999). Furthermore, The Jamaican frog *Eleutherodactylus cundalli* transport their tadpoles after hatching from the breeding caves to forest feeding habitats. The humid environment of caves is optimal for egg development, although the food resources for hatched young are extremely scarce (Diesel et al. 1995).

Movements of broods may also entail costs. For example, in ungulates and macropods with following young, weaning is delayed because young expend the energy gained from milk on movement rather than on growth (Fisher et al. 2002). sandwich tern chicks are attacked and sometimes killed by the territory owners during the movement through the colony (Stienen & Brenninkmeijer 1999). In some years, lapwing *Vanellus vanellus* broods hatched away from the feeding site have lower brood survival than those hatched close to the feeding area, because the extensive movements close after hatching are probably costly (Blomqvist & Johansson 1995).

Parents may trade off these costs against the benefits if the movements of the brood are unrestricted. Although the costs and benefits belonging to a particular habitat and their contribution to reproductive success are rarely clear (Ens et al. 1992). Furthermore, a habitat may be advantageous from one aspect, while disadvantageous from another (e.g. more abundant food may be associated with

higher predation risk; Houston et al. 1993). Therefore, the choice of brood-rearing habitat may influence the survival and growth of the offspring, and it may also affect behaviour.

In this study we investigate the parental dilemma of where to rear their young, in a small shorebird, the Kentish plover *Charadrius alexandrinus* (body mass ca. 40 g). Kentish plovers lay their eggs on the ground and both parents incubate the clutch (Fraga & Amat 1996, Kosztolányi & Székely 2002). Their chicks are precocial and leave the nest scrape a few hours after hatching. Both parents usually attend the chicks at hatching, although as the chicks get older, either the male or the female may desert the brood (Warriner et al. 1986, Székely & Lessells 1993, Amat et al. 1999). Thus some broods are raised by both parents until the chicks fledge (in the present study 55.5%, $n = 110$ broods), whereas in others either the male (40.9%) or the female cares for the chicks (3.6%).

We investigated the Kentish plovers in Southern Turkey where they raise their young in two habitats: on the lakeshore and in the saltmarsh. The objectives of our study were to determine the distribution of broods between the two brood-rearing habitats over the breeding season, and to evaluate the consequences of brood movement on parental care. Firstly, we showed that the broods move between these habitats and broods hatched late in the season concentrated on lake shore. Secondly, we tested two hypotheses why broods moved toward the lakeshore: (i) the ambient environment is harsher in the saltmarsh than on the shore, (ii) the saltmarsh provides less food than the shore, particularly late in the breeding season when it dries out. Thirdly, if competition for food is more intense in the shore, particularly late in the season, then this should influence the parental behaviour and the timing of brood desertion. Specifically, we predicted that females, which desert more often the brood than males, will stay with their chicks for longer on the shore to defend them from neighbouring families.

Methods

Fieldwork was carried out at Lake Tuzla (36° 43' N, 35° 03' E), southern Turkey (see Székely & Cuthill 1999, Székely et al. 1999) between 13 April and 16 July (1996), 15 April and 30 June (1997), 8 April and 10 July (1998) and 14 April and 8 July (1999). The Kentish plovers reared their chicks in two types of habitats: (i) shore, i.e. the north edge of Lake Tuzla, and (ii) saltmarsh, alkaline grassland of *Salicornia europaea* and *Antrochneum fruticosum* situated in a 50 – 200 m strip on the north side of the lake. Lake shore also included mudflats at the edge of the lake and edges of temporary pools that dried out by late June. Saltmarsh also included dry habitats such as neighbouring arable land.

Both parents were caught and ringed with a metal ring and a unique combination of colour rings. Chicks were ringed either in the nest scrape, or if they already left nest scrape we ringed them at the first encounter. The age of the latter broods was estimated using the length of their right tarsus (see Székely & Cuthill 1999). We studied 144 broods altogether. We attempted to visit each brood every other day until the chicks died, or they reached the age of 25 days. During these visits the number and sex of attending parent(s) and the type of brood-rearing habitat were recorded. Behavioural records were taken for 1 – 2 h every 4 – 6 days by scanning the behaviour of parents and of chicks every 30 s (see Székely & Cuthill 1999). The density of plovers was estimated only in 1998 by recording the number of Kentish plovers in a 25 m radius around focal broods every 5 min. The habitat of broods during the behavioural observations was also recorded. Ambient temperature was measured to the nearest 0.1 °C at ground level at the end of behavioural observations.

Statistical analyses

We considered each brood as the unit of analyses. If more than one record was available for a brood, we took the mean of these records. Dates were calculated as the number of days since 1st March. Hatching dates and dates of behavioural observations did not differ between years (one-way ANOVAs, hatching date: $F_{3,140} = 0.746$, $P = 0.527$; date of behavioural observations: $F_{3,140} = 0.405$, $P = 0.749$), thus we did not consider year-effects in the analyses. Nevertheless, we tested the robustness of our conclusions by including year in all models of temperature, plover density and behaviour (results not shown), and in all cases our conclusions have remained unaltered.

Brood-rearing habitat was calculated in two ways. First, in the analysis of movement of broods and of desertion we used it as a continuous variable, i.e. brood-rearing habitat was the proportion of time each family spent on the shore during brood visits. Second, habitat was treated as a dichotomous variable in analyses of data collected during behaviour samples. During the behavioural observations 22 broods out of 144 stayed only on the shore and 36 stayed only in saltmarsh, whereas 86 spent some time in both habitats. For the latter broods the habitat where they spent more time was selected, and only the behavioural records were included in the analyses that were collected in the corresponding habitat.

Kentish plovers are insectivorous (Cramp & Simmons 1983), and they feed with a characteristic run-and-peck style by taking food items from the ground, vegetation, or water. They may also catch preys such as flies from the air. We use feeding efficiency ($\text{no. of pecks} \times 10^2 \times (\text{no. of pecks} + \text{no. of runs})^{-1}$) as a measure of food abundance because foraging rates may be better estimates of the foraging value of habitats than standard arthropod sampling methods (Palmer et al.

2001). If feeding efficiency is close to 0, then the plover work hard to get a food item, whereas a value close to 100 indicates abundant food. The plover density was calculated as number of plovers * ha⁻¹. Brooding by a parent was defined as percent of time it brooded at least one chicks, whereas brooding of chicks was defined as percent of time when the chick was brooded. Fighting and feeding were defined as percent of time a bird spent on fighting and feeding, respectively.

We analysed temperature, plover density and behavioural data by general linear models (GLMs). For the analyses of temperature, plover density and feeding efficiency of parents, habitat (factor), observation date (covariate), and their interaction were included in the models. In the analyses of feeding, fighting, brooding and chick feeding efficiency, we also included brood age (covariate) in the GLMs. In these models, we tested the differential effects of brood-rearing habitats over the breeding season by the interaction between observation date and habitat. Temperature was $\lg_{10}(x+1)$ transformed and behavioural variables (brooding, fighting, feeding and feeding efficiency) were *arcsine-square root* transformed (Sokal & Rohlf 1995). The variance of plover density was not constant between the habitats, therefore we used gamma error distribution in the analyses of plover density (Crawley 1993). Behavioural variables were also analysed by MANOVAs; we quote the F values associated to Wilks' λ statistic and the probability of the F -tests (Norušis 1994).

Duration of parental care was investigated only for females, because desertion by males was rare (see above). Duration of biparental care (response variable, in days) was analysed by a GLM model where brood rearing habitat (proportion of time on the shore, covariate) and observation date (covariate) were included in the model for broods in which either the female deserted the brood, or both parents stayed with their chicks for at least 25 days. These analyses, however, may be biased because they did not include those broods that died whilst the female still attended the brood. Thus we also analysed duration of biparental care by Cox regression (Norušis 1994) in which the response variable was the duration of biparental care, the terminal event was desertion by the female, and both habitat and observation date were covariates. Cases were censored if biparental care lasted for 25 days or chicks died whilst both parents attended.

We carried out several experimental brood manipulations during the study (e.g. Székely & Cuthill 1999, Székely & Cuthill 2000) and these manipulations may potentially influence our results. However, we found no evidence that the behaviour of parents (MANOVAs, 1996 – 1999, males: Wilks' $\lambda = 0.671 - 0.918$, $P = 0.373 - 0.980$; females: Wilks' $\lambda = 0.705 - 0.751$, $P = 0.094 - 0.595$), the behaviour of their chicks (Wilks' $\lambda = 0.832 - 0.959$, $P = 0.427 - 0.972$) or the use of brood-rearing habitat (one-way ANOVAs, 1996 – 1999, $P = 0.201 - 0.924$) was influenced by these manipulations.

Statistical analyses were carried out using SPSS for Windows 8.0 (Norušis 1994) and R 1.6.1 for Windows (Ihaka & Gentleman 1996). We used Type III sum of squares. Two-tailed probabilities and means \pm SE are given.

Results

Movement of broods

116 broods out of 144 were observed in both habitats, 22 broods stayed only in the saltmarsh, whereas 6 stayed only on the shore. The first observed habitat change of 95 broods out of the 116 was toward the shore (Binomial test, $P < 0.001$), and these broods spent more time on the shore as the season proceeded ($B = 0.005 \pm 0.002$, $t_{114} = 3.349$, $P = 0.001$).

Factors influencing the movement of broods

Temperature

Ambient temperatures increased from April till June/July (linear regression on the shore: $B = 0.002 \pm 0.0004$, $t_{74} = 4.275$, $P < 0.001$, in the saltmarsh: $B = 0.002 \pm 0.0004$, $t_{68} = 5.519$, $P < 0.001$). Nevertheless, temperature is unlikely to explained the movement of broods between saltmarsh and lakeshore, because neither the slopes nor the intercepts of temperature over the breeding season were different between two types of habitats (GLM, difference between intercepts: habitat, $F_{1,140} = 0.124$, $P = 0.725$; difference between slopes: habitat*observation date interaction, $F_{1,140} = 0.024$, $P = 0.877$).

Feeding efficiency

Feeding efficiency of males, females and their chicks showed a consistent pattern (Fig. 1). Firstly, feeding efficiency was higher on the shore (males: 32.4 ± 1.79 , $n = 72$; females: 25.3 ± 1.85 , $n = 68$; chicks: 27.1 ± 1.10 , $n = 76$) than in the saltmarsh (males: 14.1 ± 1.58 , $n = 58$, $t_{128} = 7.581$, $P < 0.001$; females: 9.7 ± 1.20 , $n = 55$, $t_{121} = 6.811$, $P < 0.001$; chicks: 12.2 ± 0.94 , $n = 68$, $t_{142} = 9.595$, $P < 0.001$). Secondly, feeding efficiency decreased significantly or marginally significantly in the saltmarsh over the season, whereas it tended to increase on the shore, that is, the direction of change tended to be different in the two habitats (Fig. 1, GLM, habitat*observation date interactions, males: $F_{1,126} = 5.606$, $P = 0.019$; females: $F_{1,119} = 3.365$, $P = 0.069$; chicks: $F_{1,139} = 2.992$, $P = 0.086$).

Plover density

The density of plovers was higher on the shore (8.1 ± 1.78 plovers/ha, $n = 22$) than in the saltmarsh (3.0 ± 0.36 plovers/ha, $n = 24$, GLM with gamma errors, $F_{1,44} = 15.336$, $P < 0.001$), and this difference is particularly strong in late broods (Fig. 2). There was a significant increase in the density of plovers on the shore over the breeding season, whereas the density appeared to stay constant in the saltmarsh (Fig. 2, GLM, habitat*observation date interaction: $F_{1,42} = 7.489$; $P = 0.009$).

Behaviour of parents and their chicks

Males, females and their chicks spent more time on feeding on the shore than in the saltmarsh, and the difference between habitats increased over the breeding season (Table 1, Fig. 3 and Fig. 4). Also, parents of both sexes spent more time fighting on the shore than in the saltmarsh, and this difference tended to increase over the season in females (Table 1, Fig. 3). In contrast, brooding time was higher in the saltmarsh than on the shore (Table 1, Fig. 3, Fig. 4).

These results were consistent with multivariate tests that showed a significant or marginally significant interactions between observation date and habitat (Table 2).

Brood desertion by females

Duration of biparental care increased with time spent on the shore and biparental care lasted for longer in late broods than in early ones (GLM, time spent on the shore: $F_{1,68} = 13.600$, $P < 0.001$; observation date: $F_{1,68} = 23.043$, $P < 0.001$).

The results of these analyses are consistent with survival analysis of female desertion, because the duration of biparental care increased with both the percent of time spent on the shore and with observation date (Cox regression, time spent on the shore: $B = -1.96 \pm 0.586$, Wald = 11.154, $df = 1$, $P = 0.008$; observation date: $B = -0.04 \pm 0.012$, Wald = 14.210, $df = 1$, $P = 0.002$). That is, parents stayed together for longer in families that spent more time on the shore, especially late in the season.

Discussion

Kentish plover parents took their chicks toward the shore after hatching, and they spent more time on the shore as the season proceeded. This cannot readily be explained by ambient temperature, because temperature was similar in both habitats. Available food (estimated by feeding efficiency) was similar in the

habitats at the beginning of the season; however, it decreased (significantly or marginally significantly) in both parental sexes and the chicks in the saltmarsh, whereas it tended to increase on the shore. The decrease of available food in the saltmarsh may be explained by the drying out of this habitat (pers. obs.). As the food density in the saltmarsh decreased, parents moved with their chicks toward the shore, and therefore the density of plovers increased on the shore.

The difference in environment influenced the behaviour of birds. Because of the higher breeding density on the shore, parents fought more with other plovers. Both parents and chicks fed more on the shore, because food abundance was higher. Brooding time of parents and chicks was higher in the saltmarsh. This may be explained in different ways: (i) Parents on the shore had no time and/or energy to brood because of the higher fighting time. (ii) Chicks in the saltmarsh fed less, therefore grew slowly, and therefore they needed more brooding. (iii) If a brood was only temporarily on the shore, it was more profitable for both parents and chicks to feed during that time than to brood. The length of biparental care was in accordance with density and fighting time. Because of higher competition, longer biparental care was needed to raise the brood successfully in families that spent more time on the shore.

Like Kentish plovers, piping plover broods *Charadrius melodus* choose habitats for feeding where arthropod abundance is high (Elias et al. 2000). The foraging rates of chicks were also highest in these habitats. However, in this study the density and interactions between plovers on feeding habitats were not estimated. semipalmated plovers *Charadrius semipalmatus* in Canada nests on inland and coastal habitats. Blanken & Nol (1998) found no difference in foraging and brooding time of parents between the two kind of habitats; however, coastal parents fought more, probably because of the higher density of feeding broods. In the latter study the two kinds of habitats were far from each other, broods did not move between habitats and inland habitats also contained ponds, although with less food than the coastal mudflats. Our result and the result of Blanken & Nol (1998) concerning density dependent fighting is in accordance with an experiment carried out in lesser snow goose *Anser caerulescens caerulescens* during brood-rearing. Mulder et al. (1995) manipulated food availability by creating high-biomass food patches. In these patches the density of geese was higher than in control patches and the social interactions between families and pairs were also more frequent.

In conclusion, our study suggests that Kentish plovers choose brood rearing habitat depending on food availability and that this choice influences the behaviour. Specifically, broods moved toward the shore where more food was available and this movement resulted in higher densities and more fighting on the shore; furthermore the length of biparental care also increased. The results arouse several questions for future studies. First, are chick growth and/or survival

influenced by brood-rearing habitat? For example, Elias et al. (2000) found some evidence for different survival rates in piping plovers feeding in different habitats. Secondly, if more food is available on the shore, why do some families spend more time in the saltmarsh? Is this a result of a difference between parents, space limitations on the shore, or are the costs of habitat change high for some families?

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Table 1. Behaviour of parents and their chicks on the lakeshore and in the saltmarsh (mean \pm SE)

	Shore % of time	Saltmarsh % of time	<i>t</i> -test	
			<i>t</i>	<i>P</i>
Males (72, 58)*				
Brooding	7.4 \pm 1.28	21.4 \pm 2.50	5.819	< 0.001
Fighting	11.9 \pm 1.24	6.2 \pm 0.65	4.055	< 0.001
Feeding	12.7 \pm 1.01	5.1 \pm 0.71	6.605	< 0.001
Females (68, 55)*				
Brooding	12.6 \pm 1.64	23.4 \pm 2.58	3.542	0.001
Fighting	10.3 \pm 0.97	5.8 \pm 0.81	3.708	< 0.001
Feeding	7.5 \pm 0.72	2.5 \pm 0.40	6.528	< 0.001
Chicks (76, 68)*				
Brooding	13.6 \pm 1.64	33.2 \pm 2.68	6.238	< 0.001
Feeding	15.4 \pm 0.79	6.2 \pm 0.57	9.394	< 0.001

* Number of broods on the lakeshore and in the saltmarsh, respectively.

Table 2. Behaviour of Kentish plover parents and their chicks in relation to brood-rearing habitat, date of observation and brood age (general linear models).

	Habitat	Observation date	Brood age	Observation date * Habitat
(variable <i>df</i> , error <i>df</i>)	<i>F</i> (<i>P</i>)	<i>F</i> (<i>P</i>)	<i>F</i> (<i>P</i>)	<i>F</i> (<i>P</i>)
Males				
Multivariate tests (3, 123)	2.961 (0.035)	1.656 (0.180)	5.289 (0.002)	2.684 (0.050)
Univariate tests (1, 125)				
Brooding ($r^2 = 0.315$)	6.424 (0.012)	0.598 (0.441)	15.124 (< 0.001)	4.121 (0.044)
Fighting ($r^2 = 0.142$)	2.707 (0.102)	2.880 (0.092)	0.720 (0.398)	1.189 (0.278)
Feeding ($r^2 = 0.289$)	0.731 (0.394)	0.626 (0.430)	1.781 (0.184)	2.908 (0.091)
Females				
Multivariate tests (3, 116)	1.715 (0.168)	1.152 (0.331)	5.233 (0.002)	3.434 (0.019)
Univariate tests (1, 118)				
Brooding ($r^2 = 0.226$)	0.073 (0.788)	2.764 (0.099)	15.896 (< 0.001)	0.018 (0.895)
Fighting ($r^2 = 0.140$)	2.119 (0.148)	0.678 (0.412)	0.436 (0.510)	3.478 (0.065)
Feeding ($r^2 = 0.311$)	3.195 (0.076)	0.582 (0.447)	0.023 (0.881)	7.311 (0.008)
Chicks				
Multivariate tests (3, 138)	1.830 (0.164)	1.629 (0.200)	13.240 (< 0.001)	2.950 (0.056)
Univariate tests (1, 139)				
Brooding ($r^2 = 0.313$)	1.890 (0.171)	3.037 (0.084)	15.049 (< 0.001)	0.724 (0.396)
Feeding ($r^2 = 0.485$)	0.731 (0.394)	0.004 (0.949)	19.662 (< 0.001)	3.663 (0.058)

Figure legends

Fig. 1. Feeding efficiency (no. of pecks * 10^2 * (no. of pecks + no. of runs)⁻¹) of male (A), female (B), chick (C) Kentish plovers on the shore (dots and solid line) and in the saltmarsh (open circles and broken line, *arcsine-square root* transformed). Slopes of linear regression lines: male, shore: $B = 0.14 \pm 0.103$, $t_{70} = 1.312$, $P = 0.194$, saltmarsh: $B = -0.21 \pm 0.101$, $t_{56} = 2.040$, $P = 0.046$; female, shore: $B = 0.09 \pm 0.116$, $t_{66} = 0.780$, $P = 0.438$, saltmarsh: $B = -0.18 \pm 0.093$, $t_{53} = 1.964$, $P = 0.055$; chick, shore: $B = 0.09 \pm 0.062$, $t_{74} = 1.471$, $P = 0.146$, saltmarsh: $B = -0.13 \pm 0.067$, $t_{66} = 1.923$, $P = 0.059$.

Fig. 2. Seasonal variation in density (plovers/ha) on the shore and in the saltmarsh (see Fig. 1 for legend, GLM with gamma errors, shore: $B = 0.55 \pm 0.221$, $t_{20} = 2.449$, $P = 0.021$, saltmarsh: $B = 0.002 \pm 0.0267$, $t_{22} = 0.085$, $P = 0.933$).

Fig. 3. Parental behaviour on the shore and in the saltmarsh: brooding (A & B), fighting (C & D) and feeding (E & F, see Fig. 1. for legend, *arcsine-square root* transformed). Slopes of linear regression lines: male brooding, shore: $B = 0.03 \pm 0.121$, $t_{70} = 0.275$, $P = 0.784$, saltmarsh: $B = -0.23 \pm 0.135$, $t_{56} = 1.719$, $P = 0.091$; female brooding, shore: $B = -0.25 \pm 0.131$, $t_{66} = 1.932$, $P = 0.058$, saltmarsh: $B = -0.10 \pm 0.142$, $t_{53} = 0.730$, $P = 0.469$; male fighting, shore: $B = -0.14 \pm 0.087$, $t_{70} = 1.550$, $P = 0.126$, saltmarsh: $B = -0.03 \pm 0.055$, $t_{56} = 0.593$, $P = 0.556$; female fighting, shore: $B = 0.157 \pm 0.079$, $t_{66} = 1.985$, $P = 0.051$, saltmarsh: $B = -0.06 \pm 0.071$, $t_{53} = 0.903$, $P = 0.371$; male feeding, shore: $B = 0.06 \pm 0.077$, $t_{70} = 0.794$, $P = 0.430$, saltmarsh: $B = -0.13 \pm 0.064$, $t_{56} = 1.999$, $P = 0.050$; female feeding, shore: $B = 0.08 \pm 0.066$, $t_{66} = 1.212$, $P = 0.230$, saltmarsh: $B = -0.14 \pm 0.047$, $t_{53} = 3.073$, $P = 0.003$.

Fig. 4. Chick behaviour on the shore and in the saltmarsh: brooding (A) and feeding (B, see Fig. 1. for legend, *arcsine-square root* transformed). Slopes of linear regression lines: brooding, shore: $B = -0.17 \pm 0.127$, $t_{74} = 1.329$, $P = 0.188$, saltmarsh: $B = -0.19 \pm 0.127$, $t_{66} = 1.529$, $P = 0.131$; feeding, shore: $B = 0.11 \pm 0.054$, $t_{74} = 2.127$, $P = 0.037$, saltmarsh: $B = -0.08 \pm 0.052$, $t_{66} = 1.574$, $P = 0.120$.

Fig. 1.

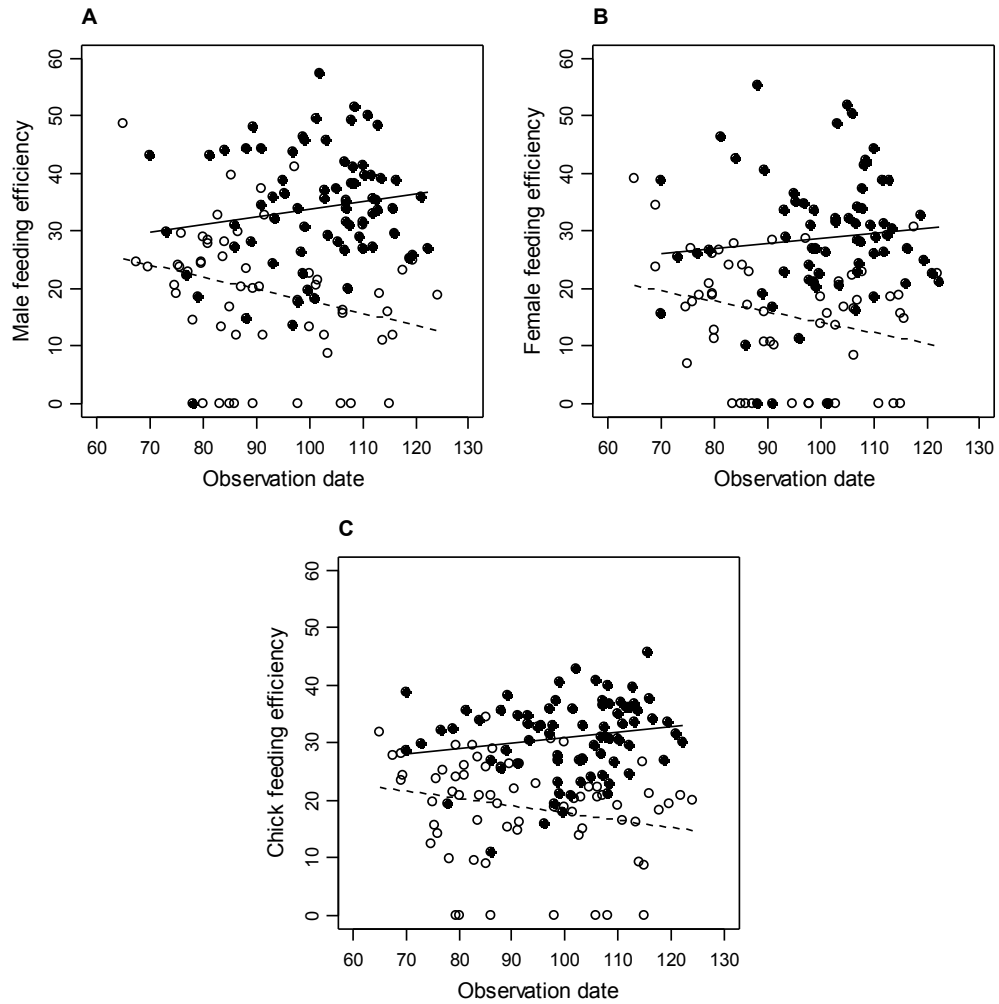


Fig. 2.

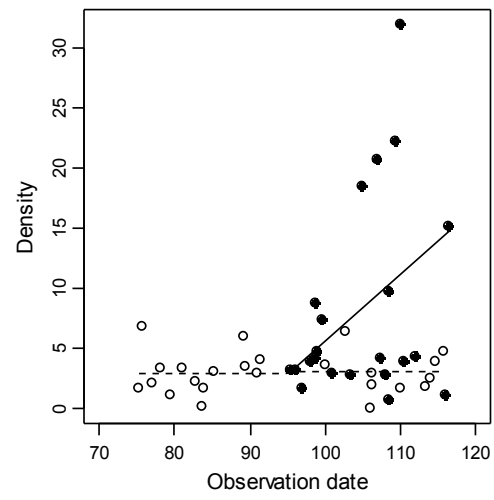


Fig. 3.

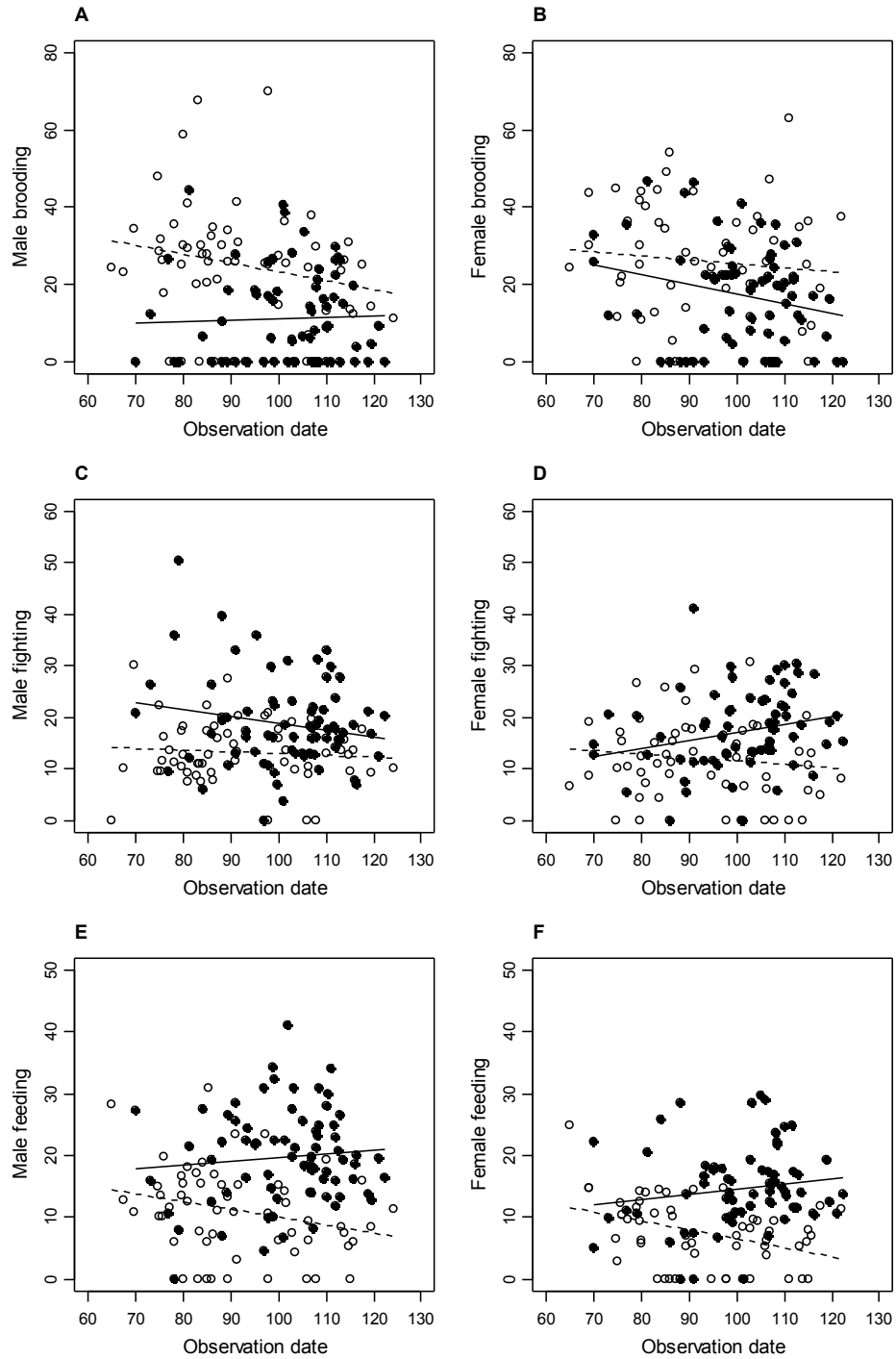
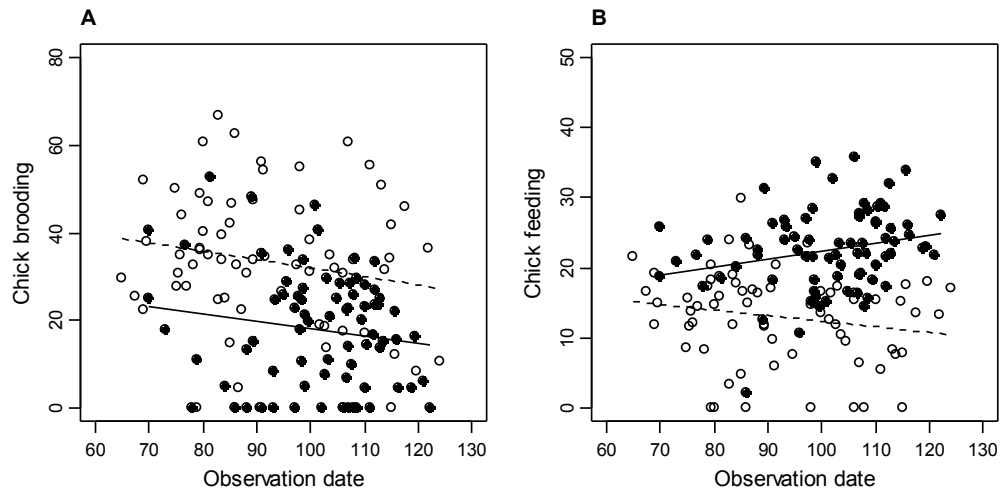


Fig. 4.



Summary

Parental care is often costly, since the resources invested in raising the current offspring may be diverted from producing offspring in future. This creates an interesting situation whereby the male and the female have shared interest in raising their common young, although each parent would do it better if the other parent does the hard work. This opposite interest of the sexes lead to a sexual conflict over care. In my thesis I investigate this sexual conflict, in particular, how the costs and benefits of parental care influence caring decisions in the Kentish plover *Charadrius alexandrinus* during incubation and brood rearing.

First, I review the theoretical and empirical studies of care. I evaluate how different factors, such as the number of young or food availability influence parental behaviour. I argue that parental care and mating decisions are interrelated, and thus should be investigated within one theoretical framework. I outline two theoretical approaches of parental care: single-sex and game-theoretic models, and present an experimental test of a game-theoretic model. I point out that studies of paternity and paternal care produced contradictory results. Finally, I illustrate the power of phylogenetic comparative methods using selected case studies.

Second, I evaluate the various costs and benefits of parental care in a small precocial wader with a highly variable parental care pattern, the Kentish plover. In this species both parents incubate the clutch, although after hatching either the female or the male may desert the brood and remate. Thus biparental care, male-only and female-only care all occur in the same population at the same time. This diversity makes this species suitable for studying costs and benefits of parental care.

Using an automatic recording device (the transponder system) I report the pattern of incubation for the full day. Incubation constancy was high over the whole day, although the sexes had a different incubation pattern: females incubated mostly during daytime, whereas males incubated mostly at night. I propose that the different conspicuousness of male and female plovers to visually searching nest predators, or the different predator detecting ability of sexes may explain the diurnal pattern of incubation.

Incubating females cannot replenish their energy reserves, therefore a decrease in their body mass is expected during the day. This proposition was confirmed by repeated captures of a set of females. Female body mass decreased by 8.4% from morning to afternoon and this decrease is consistent with the notion that incubation is costly. However, the alternative explanation of strategic body mass regulation cannot be ruled out.

If incubation is a costly behaviour, then it seems beneficial to desert during incubation provided that one parent is able to incubate and hatch the eggs on its alone. I investigated this proposition by a mate-removal experiment in which the male or the female was removed for a short period of time. At some nest I provided supplementary food for the remaining parent. As expected, total incubation time decreased at uniparental nests. However, food supplementation did not attenuate this decrease. I conclude that offspring desertion during incubation may be a more costly behaviour than desertion after hatching, since one parent is unable to sustain a sufficient level of incubation.

Kentish plovers rear their broods in two types of habitat in southern Turkey: on the lakeshore and in the saltmarsh. Each year the saltmarsh dried out by late June. I found that families moved between these habitats, and as the season progressed they spent more time on the shore. This shift may be explained by different food availabilities: the families moved toward the shore, because food intake was higher on the shore than in the saltmarsh, particularly late in the season. Thus the broods were concentrated on the shore, and this influenced their behaviour. Parents spent more time on fighting with neighbouring broods on the shore. Furthermore, biparental care lasted for longer on the shore, probably because two parents were needed to defend the feeding territory of the family. These results suggest that the spatial and temporal distribution of resources appear to influence the patterns of brood care.

In conclusion, my thesis produced novel insights on parental care. First, in the parental care review I investigated this behaviour from several perspectives using, in particular, empirical, theoretical and phylogenetical approaches. Second, observational and experimental studies in the Kentish plover found new aspects of incubation and brood-rearing behaviour and they identified certain costs and benefits of their parental care for the first time.

Összefoglalás

Az utódgondozó viselkedés ez egyik legváltozatosabb jelleg az állatvilágban. Mind a gondozás formája, mind a hossza, mind a gondozó szülők száma és neme nagy változatosságot mutat. Az utódgondozás nyilvánvaló haszna az utódok jobb túlélése. Az utódok gondozására fordított véges forrásokat azonban nem lehet más leszármazottakra fordítani, ezért az utódgondozás költséges lehet. A költségek megléte miatt mindkét szülőnek az érne meg jobban, ha a másik szülő bajlódna a közös utódok felnevelésével, míg önmaga a forrásait saját túlélésére vagy további utódok létrehozására fordítaná. Ezért a két szülő között konfliktus állhat fenn arra nézve, hogy ki nevelje fel az utódokat. Valószínűleg ez a konfliktus, illetve a feloldása vezet az utódgondozás állatvilágban tapasztalható nagyfokú változatosságához.

Értekezésemben azt vizsgálom, hogy az utódgondozással járó költségek és hasznok hogyan befolyásolják a szülők döntéseit a gondozás mértékéről, azaz a szülők hogyan oldják meg a nemek közötti konfliktust. Az értekezés két fő részre tagolódik: (a) az utódgondozó viselkedés áttekintésére és (b) egy, a széki lilén *Charadrius alexandrinus* elvégzett terepi vizsgálatsorozatra.

Az utódgondozást áttekintő részben bemutatom, hogy miért van konfliktus a szülők között az utódgondozás terén. Áttekintem az utódgondozás változatosságának kapcsolatát a párzási rendszerek változatosságával. Felsorolom, hogy mely költségek és hasznok befolyásolhatják a gondozás mértékét. Például, hogyan hat a gondozás mértékére az egy szaporodási ciklusban létrehozott utódok száma vagy a lehetséges partnerek száma.

Egy-egy példán keresztül bemutatom az utódgondozó viselkedést leíró elméleti modellek két ágát. Az egyszülős modellek egyetlen egyed, illetve nem viselkedését vizsgálják a különböző ökológiai tényezők függvényében, míg a játékelméleti modellekben az egyedek viselkedését a másik nem, illetve a populáció többi tagja viselkedésének függvényében vizsgálják. Kitérek a modellek tesztelhetőségével kapcsolatos problémákra, és részletesen ismertetem egy játékelméleti modell tesztelését.

Az új molekuláris biológiai módszerek segítségével sok madárfajnál kimutatták, hogy a fészekalj tartalmazhat páron kívüli párzásból származó utódokat. Ilyenkor a hímek utódgondozása nemcsak a saját utód túlélését növeli, ezért a hímeknek valahogy védekezniük kell az elvesztegetett befektetés ellen. Ezt vagy az idegen hímek általi megtermékenyítés megakadályozásával, vagy pedig a gondozás mértékének az aktuális apaságnak megfelelő értékre állításával lehet elérni. A várakozásokkal ellentétben azonban a megfigyeléses, kísérletes és

összehasonlító vizsgálatok nem mindig mutattak pozitív kapcsolatot az apaság és az utódgondozás mértéke között, melynek lehetséges okaira kitérek.

Az utódgondozás megértéséhez nem csak a jelenleg ható szelekciós tényezőket fontos ismerni, hanem az adott élőlénycsoport utódgondozásának evolúciós múltját is. Két példán keresztül bemutatom, hogy a modern filogenetikai összehasonlító módszerek segítségével egyrészt hogyan lehet az utódgondozás evolúciója során lezajlott átalakulásokat rekonstruálni, másrészt hogyan lehet a különböző ökológiai és életmentet-tényezőknek az utódgondozó viselkedésre tett hatást vizsgálni rokon fajokon.

Az értekezésem második részében a széki lilék kotlási és fiókanevelési viselkedését vizsgálom. A széki lile egy kistermetű (kb. 40-44 g) partimadár melynek utódgondozó viselkedése az egyik legváltozatosabb a madarak között. Az általában három tojásból álló fészkaljat mindkét szülő kotolja, azonban a fészekhagyó fiókák kikelése után az egyik szülő rendszerint elhagyja a családot (dezertál). A fiókákat az egyedül maradt szülő neveli kirepülésükig, míg a fiókákat elhagyó szülő újra párba állhat és új szaporodásba kezdhet. A fiókaelhagyás következtében egy populáción belül, azonos időben mind a kétszülős, mind a csak hím-, mind a csak tojógondozás is megtalálható. Az utódgondozás változatossága miatt a széki lile kitűnő modellrendszer az utódgondozással járó költségek és hasznok vizsgálatára. A terepvizsgálatokat 1996 és 1999 között a dél-törökországi Tuzla-tónál végeztem, ahol a széki lile igen gyakori fészkelő madár.

A lilék kotlási viselkedését három vizsgálatban tanulmányoztam. Elsőként egy automatikus adatrögzítő rendszert készítettem, amely képes volt a fészken ülő madarat azonosítani. A rendszer egy, a madarak farktollaira ragasztott kisméretű (0,4 g) chipből, egy a fészek alá helyezett antennából, továbbá leolvasóból, adatrögzítő számítógépből és áramforrásból állt. A rendszer megbízhatóan működött a terepen, mivel a hibás leolvasások száma, azaz amikor a rendszer nem tudta azonosítani a fészken ülő madarat, nagyon alacsony volt, a teljes idő 0,2 %-a.

Ezzel a rendszerrel és megfigyelésekkel nyert adatok segítségével elsőként sikerült leírni a széki lilék kotlási mintázatát a teljes nap folyamán. A fészkeket magas százalékban (89,4 %) kotolta vagy a hím vagy a tojó a teljes nap során, azonban a két szülő által a fészken töltött időnek szignifikáns napi ritmusa volt. A szülők az éjszakai, a kora reggeli és a déli órákban kotlották a legintenzívebben a fészkeket. Ezt a változatosságot a hőmérséklet változásával lehet magyarázni. A kotlás akkor a legintenzívebb, amikor a hőmérséklet a legalacsonyabb (éjszaka és kora reggel), illetve amikor a legmagasabb (délben), mivel a szülőknek védeniük kell a tojásokat az extrém hőmérséklettől. A szülők közötti munkamegosztás jellegzetes napi mintázatot mutatott. A tojók kotlottak nappal, míg a hímek főként éjszaka ültek a fészken. Ennek az élesen elkülönülő napi munkamegosztásnak a magyarázatára javasoltam két hipotézist, melyekhez további vizsgálatokra van szükség. A hímek éjszakai kotlásának oka lehet egyrészt, a nemek tollazatának

különbözősége. A hímek tollazata feltűnőbb, így ha ők kotlanának nappal, akkor a vizuálisan kereső predátorok könnyebben felfedezhetnék a fészket. Másrészt különbség lehet a két szülő predátor felismerési képességében. Például ha a hímek sikeresebbek éjszaka a predátorok felismerésben, akkor korábban el tudják hagyni a fészket egy predátor közeledésekor.

Mivel a tojók a nappali időszak nagy részét a fészken töltik, valószínűleg nem tudnak elég táplálékot gyűjteni a kondíciójuk fenntartásához. Széki lile tojók többszöri befogásával vizsgáltam, hogyan változik a madarak kondíciója a nap folyamán. Minden tojó háromszor került befogásra, egyszer reggel, egyszer délben és egyszer délután. Sikertelt kimutatni, hogy a tojók tömege valóban csökken a nap folyamán, reggeltől délutánig a testtömegük 8,4 %-át veszítik el. Ennek a tömegvesztésnek a két legvalószínűbb magyarázata a zsírtartalékok csökkenése, illetve a párologtatás során történt vízvesztés. A zsírtartalékok jelentősen csökkenhetnek a kora reggeli órákban, amikor a tojásokat melengetni kell, míg a párologtatás általi vízvesztés a déli órákban lehet nagymértékű, amikor a tojásokat aktívan hűteni kell. A tömegcsökkenés arra utal, hogy a kotlás költséges a tojók számára, azonban nem zárhatjuk ki a stratégiai tömegszabályozás lehetőségét sem.

Ha a kotlás költséges a tojók számára, akkor miért nem dezertálnak a tojók már a kotlás során? A fészket elhagyó szülő nyeresége kettős. Egyrészt megszabadul a kotlás terhei alól, másrészt pedig a korán dezertáló lile nagyobb valószínűséggel talál új párt, mivel a költési szezon előrehaladtával a pártalálás esélye csökken. Ezért vizsgáltam, hogy egy szülő képes-e egyedül kotlani és kikeltetni a fiókákat. Ehhez egy kísérletet végeztem, amelyben rövid időre (átlagosan 1,6 napra) eltávolítottam az egyik szülőt a fészektől. A várakozásom az volt, hogy a kísérletesen dezertált szülő nem képes fenntartani a kotlás normális szintjét. Az egyszülős fészkek egy csoportja mellé kis tálkákban lisztkecskacokat helyeztem, melyeket a lilék készségesen elfogadtak. Ha a táplálék megszerzéséhez szükséges idő limitálja az egyedül maradt szülő kotlási idejét, akkor a többlet táplálékkal az eltávolítás hatása csökkenthető.

Az eltávolítás után a hímek, akik egyébként csak kevés időt töltenek nappal a fészken, növelték a nappali kotlásukat, azonban a tojók kotlása nem változott. Így az eltávolítás után nem volt különbség a hímek és tojók nappali kotlási idejében. A predikcióknak megfelelően, az egyedül kotlott fészkeknél a kotlási idő alacsonyabb volt (46,9 %), mint a kétszülős kontroll fészkeknél (69,1 %). Ez azt jelenti, hogy még ha egy szülő képes is a tojásokat az embrionális fejlődéshez szükséges hőmérsékleti tartományon belül tartani, a csökkent kotlási idő miatt az embrionális fejlődés lelassulhat. Ez pedig a kotlási időszak meghosszabbodását eredményezi, és így a tojások hosszabb ideig vannak kitéve a predációs veszélynek, ami a széki lile fészkek esetén igen magas. A többlet tápláléknak azonban nem volt hatása a kotlási viselkedésre, aminek a két legvalószínűbb magyarázata, hogy egyrészt a lisztkecska nem elég változatos táplálék a lilék

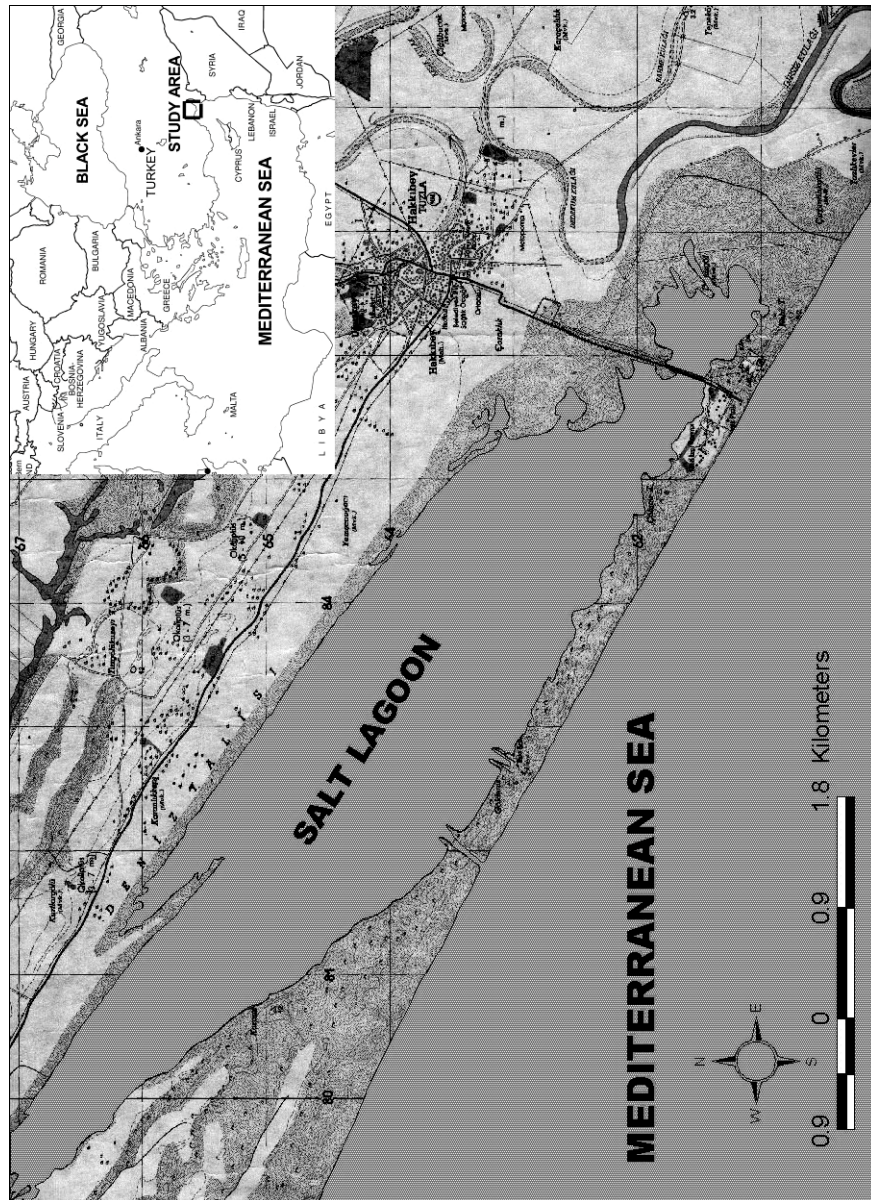
számára, másrészt nem az energetikai szükségletek modulálják a kotlási mintázatot. A kísérlet eredményei alapján arra a következtetésre jutottam, hogy a dezertálás a kotlás során költségesebb lehet, mint a fiókanevelési időszakban.

A negyedik terepi vizsgálatban a széki lilék fiókanevelési időszak alatti utódgondozó viselkedését vizsgáltam. A széki lilék két különböző élőhelyen vezetgették a fiókáikat a kelés után: a tóparton és a tóparttól távolabbi szikes területeken. A tópart az egész költési szezon során nedves maradt, a szikes területek azonban a szezon végére kiszáradtak. Egyedileg jelölt szülők és fiókák mozgását figyelve a két területen azt tapasztaltam, hogy a családok mozognak a két típusú élőhely között, és a költési szezon előrehaladtával egyre több időt töltenek a parton. Ennek oka a rendelkezésre álló táplálék mennyiségének különbségében keresendő. A parton a fiókák az idejük 15,4 %-ában csippentettek táplálékért, míg ez a szám csak 6,2 % volt a szikesen. A szezon során a táplálék mennyisége csökkent a szikesen, míg a parton kissé emelkedett. A szikesen tapasztalt táplálékcsökkenés hatására a családok egyre több időt töltöttek a parton, ezért itt növekedett a családok denzitása, ami pedig hatással volt a lilék viselkedése. A parton a szülők többet verekedtek a szomszédos lileszülőkkel. A több verekedés befolyásolta a kétszülős gondozás hosszát is: a parton több időt töltő családokban tovább maradt együtt mindkét szülő, mivel valószínűleg mindkettejükre szükség volt a táplálkozási terület fenntartásához. Mindezek arra utalnak, hogy az élőhelyek ökológiai és szociális tényezői befolyásolhatják az utódgondozó viselkedés mintázatát.

Összefoglalva, az értekezésemben ismertetett kutatások során több új eredmény született. Egyrészt az utódgondozási viselkedés áttekintése során mind empirikus, mind elméleti, mind filogenetikai szempontból vizsgáltam ezt a viselkedést. Másrészt a széki lile megfigyeléses és kísérletes terepi vizsgálatával sikerült leírni az utódgondozás eddig még nem pontosan ismert mintázatait, és sikerült azonosítani a gondozással együtt járó olyan költségeket és hasznokat, amelyek befolyásolhatják a szülők utódgondozó döntéseit. Az eddigi eredmények további érdekes kérdéseket vetnek fel, melyek közül talán a legizgalmasabb, hogy mi a dinamikája a két nem közötti konfliktus feloldásának. Melyik nem dönt előbb a gondozás mértékéről? A másik nem csak elszenvedője a döntésnek? Vagy esetleg az egyes nemek gondozási szintje egy hosszú „egyezkedési” folyamat végeredménye?

Appendix A

Map of the study area in southern Turkey



Appendix B

Female Kentish plover on her nest (photograph by János Kis)



Appendix C

Kentish plover nest with a freshly hatched chick
(photograph by András Kosztolányi)



Costs and benefits of parental care in the Kentish plover *Charadrius alexandrinus*

Az utódgondozás költsége és haszna a széki lilénél *Charadrius alexandrinus*

Értekezés a doktori (PhD) fokozat megszerzése érdekében
a biológia tudományágban

Írta: Kosztolányi András okleveles biológus

Készült a Debreceni Egyetem Biológia Doktori Iskolája
(Biodiverzitás programja) keretében

Témavezető: Dr. Székely Tamás

A doktori szigorlati bizottság:

elnök: Dr.

tagok: Dr.

Dr.

A doktori szigorlat időpontja: 200...

Az értekezés bírálói:

Dr.

Dr.

Dr.

A bírálóbizottság:

elnök: Dr.

tagok: Dr.

Dr.

Dr.

Dr.

Az értekezés védésének időpontja: 200...

