



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

PhD thesis

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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 *Laroidae*, 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), 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 *Arthrocnemum 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), 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. 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 ($11.3 \text{ h} \cdot \text{day}^{-1}$) than males ($9.4 \text{ h} \cdot \text{day}^{-1}$) 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* (Kálás & 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. &

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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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