Parental behaviour of Kentish plover
and northern lapwing

Outline of PhD thesis

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Budapest, 2003
I. Introduction

Parental care may not always be beneficial to parents. It is expected to occur when the benefits of care exceed its costs. Parental care may be beneficial in augmenting offspring survival\(^1\). The costs of care include time and energy invested in raising the offspring, the risk of injury when defending offspring against predators and lost mating opportunities whilst caring for progeny\(^2\). Parents may prematurely terminate care and abandon their young (offspring desertion)\(^3\). Desertion may be beneficial when parents are unable to increase survival chances of their offspring by providing more care, or the costs of care are excessive.

The objective of my thesis is to investigate the costs of parental care and the costs and benefits of offspring desertion. I studied two closely related waders, the northern lapwing *Vanellus vanellus*, henceforward lapwing (Appendix 1. in the Thesis), and the Kentish plover *Charadrius alexandrinus* (Appendix 2.). My research on lapwings focused on nest defence behaviour, whereas I investigated the variable parental care of Kentish plover, including male-only, female-only and biparental care. In the Kentish plover both parents incubate the clutch\(^4,5\) but one parent, more often the female, typically deserts the brood after hatching and may remate with a new partner\(^6,7\). My work follows-up previous studies in the Kentish plover\(^7\) by focusing on the benefits of care in terms of parent-offspring genetic relatedness and on remating opportunities of males and females and its causes.
II. The aims of the thesis

I focus on two aspects of parental care: (i) the benefits of care, and (ii) the costs and benefits of offspring desertion. I hypothesised that (i) the benefits of care (1) depend on the value of offspring. I analysed antipredatory behaviour in lapwings, and I predicted that parents invest more in defence of those offspring that have higher survival chances. I compared defence behaviour between the sexes. Since males tend to be larger than females, if body size relates to the effectiveness of defence, then males should defend their nests more intensively than females. (2) Benefits of care may be modulated by the genetic relatedness between parents and offspring, since the care-giver is often not the genetic parent. Contrary to the social mating system, the genetic mating system has not yet been studied up to date in the Kentish plover. I investigated the frequency of extra-pair chicks in broods to study extra-pair paternity and maternity. (3) I also studied genetic relatedness of parents in relation to the distribution of extra-pair chicks in the broods of Kentish plover and two other waders, the common sandpiper Actitis hypoleuca and the western sandpiper Calidris mauri. High genetic relatedness between parents may lead to the accumulation of deleterious alleles in offspring (inbreeding depression). I expected that waders unable to find an unrelated partner are more likely to engage in extra-pair matings to avoid the cost of inbreeding.

(ii) I studied remating opportunities in the Kentish plover. (4) To explain male biased parental care i.e. females desert their broods more often than males, I hypothesised a bias between the sexes in remating
opportunities. I studied the differences of natural plumage traits between males and females. I hypothesised that males have longer flank- and breast-feathers (henceforward flank-feathers) than females, since they are more likely to care for the brood and brood the chicks, and feather quality may play an important role in heat insulation. To explain variation in male remating opportunities, I studied the effect of male plumage traits on remating time by manipulating these traits. I hypothesised that males with larger badges and longer flank-feathers need less time to remate than others, because badges may refer to good genes and feathers may refer to good parental abilities, therefore females might choose upon these traits. Finally, sex biased remating opportunities may be due to biased population sex ratio. Male biased offspring sex ratio could result in such a bias. I hypothesised that either the hatching sex ratio is male biased or male chicks survive better until fledging than females.

III. Methods

First, we investigated the response of lapwings during incubation to natural predators and to a dummy nest predator, a hooded crow *Corvus corone cornix*. We related defence behaviour to the presumed value of offspring and we compared nest defence between the sexes. Fieldwork was carried out at Miklapuszta, an alkaline grassland of about 2000 ha in Central Hungary, between 1992 and 1994 (Appendix 3.). Observations were investigated between April to June each year.
Second, further field studies were investigated in Kentish plovers on a saltmarsh of 200 ha at Lake Tuzla, Çukurova Delta, Southern Turkey, between 1996 and 1999 (Appendix 4). About 1000 pairs bred around the lake. Studies were carried out between April and June each year. (2) We collected blood samples from 89 families between 1998 and 1999. Parentage was determined with minisatellite DNA fingerprinting by Dr. D. Blomqvist and C. Küpper, Konrad Lorenz Institute for Comparative Ethology, Vienna. (3) Kentish plover, common sandpiper and western sandpiper fingerprints were scored by C. Küpper, Dr. D. Blomqvist and Dr. J.T. Lifjeld, Zoological Museum, University of Oslo.

(4) We carried out a field experiment to assess remating opportunities in 1996. We removed either the male or the female and the clutches of 40 mated pairs. We measured remating time and observed remating behaviour. (5) We studied the natural variation of flank-feather length in male plovers in 1999. (6) Then we enlarged badge size (Appendix 5.) and shortened flank-feather length in a factorial design, and recorded remating time and behaviour in 60 males. (7) To assess sex allocation in families, we collected blood samples from chicks in 210 broods between 1997 and 1999. Chicks’ sex was determined with the CHD genes by Dr. R. Griffiths, Glasgow University, UK, and Dr. S. Yezerinac Reed College, USA.
IV. Results

(1) Lapwings attacked both natural predators and the dummy crow near their nests. However, defence was not related to offspring value. Males seemed to defend clutches more intensively late in the season but this relationship was due to declining nest density. Males attacked the dummy predator more intensively than females, and we explain this sex difference by division of labour. (2) The genetic mating system of the Kentish plover was basically monogamous, although both types of extra-pair matings, extra-pair paternity (EPP) and extra-pair maternity (quasi parasitism), as well as intraspecific brood parasitism (egg dumping) were found. EPP tended to be more frequent at the end of the breeding season. (3) Our results also show that genetically related parents are more likely to engage in extra-pair mating in birds than unrelated ones. This was consistent in all three waders, supporting the inbreeding avoidance hypothesis.

(4) Male Kentish plovers took more time to find new mates than females, so the cost of lost mating opportunities due to parental care appears to be higher for females. Remating time increased during the breeding season, when the chance for renesting declines. (5) Male plovers had longer flank-feathers than females, and the profile of feather length was different for the two sexes suggesting that flank-feathers may signal male quality. (6) Cutting flank-feathers and enlarging badges did not influence male remating opportunity. However, badge-enlarged males spent less time on fighting with conspecifics than controls. This is consistent with results in passerines where melanin signals play a role in status signalling, rather than mate
(7) Brood sex ratio at hatching was not different from parity. However, the proportion of male chicks decreased over the breeding season and larger chicks tended to be more often sons than daughters. These results suggest that early hatched male chicks at an adult age are more likely to breed in their first breeding season than later hatched ones. Sons’ survival was higher until fledging than daughters’. Up to date male biased chick survival is the best explanation of a potential male biased adult sex ratio that could explain gender differences in remating and parental care in Kentish plover.

V. Conclusions

We found different parental allocation into offspring in males and females both in the lapwing and the Kentish plover. We found better remating opportunities for female than male Kentish plovers and we explain it with biased population sex ratio. Sex bias in remating opportunities may also be driven by different breeding schedule in males and females, males spending more time on reproduction in a given breeding season. I recommend further studies to reveal and understand mate choice and mate switching in Kentish plover. We also revealed the genetic mating system of Kentish plovers and showed the influence of genetic relatedness between parents on mating strategies for the first time in birds. Further tests are required to check specific assumptions with regard to inbreeding avoidance, i.e. how do Kentish plovers recognise kin.
VI. Acknowledgements  
I thank my collaborators, T. Székely, D. Blomqvist, J.C. Cuthill, A. Liker, Á.Z. Lendvai, B. Kempenaers, C. Küpper, R. Griffiths, S. Yezernica, M. Andersson, R.B. Lanctot, B.K. Sandercock and J. Wallander their contribution to this thesis. P. Kabai, A. Kosztolányi and A. Liker gave advice whilst preparing the thesis. A. Kosztolányi, Á.Z. Lendvai and I. Szentirmai helped in field work. I was supported by a PhD studentship of Eötvös University, between 1995 and 1998. Projects were supported by NERC (GR3/10957), OTKA (T020036 & T031706) to T.S. and NKB-99-KUT-3-D/04 to J.K.

VII. References

Citations

4 Kosztolányi A & Székely T 2002. Using a transponder system to monitor incubation routines of snowy plovers. J. Field Ornithol. 73, 199-205

Published papers and manuscripts included in the thesis

Numbers in parenthesis refer to chapters of the thesis throughout this outline

(i) benefits of parental care

(2) Küpper C, Kis J, Székely T, Cuthill IC & Blomqvist D. Frequency and timing of extra-pair fertilizations in the polyandrous Kentish plover *Charadrius alexandrinus*: support for sperm storage? *Behav. Ecol. Sociobiol.* under revision


(ii) costs and benefits of offspring desertion


(6) Lendvai ÁZ, Kis J, Székely T & Cuthill IC. An investigation of mate choice based on manipulation of multiple ornaments in the Kentish plover. *Anim. Behav.* accepted

(7) Székely T, Cuthill IC, Yezerniac S, Griffiths R & Kis J. Brood sex ratio in the Kentish plover. *Behav. Ecol.* in press

*Related papers and manuscripts*

birds engage in extrapair copulations: a reply to Griffith & Montgomerie.

**Nature** 422, 833-834

Bókony V, Liker A, Székely T & **Kis J**. Black plumage colouration and flight displays in plovers and allies. **Proc. R. Soc. Lond. B submitted**

**Published conference abstracts**


**Küpper C, Blomqvist D, Székely T & Kis J** 2001. Genetic parentage in a polyandrous bird, the Kentish plover. **Ethology (Supplements)** 36, 198