Final report

Life history consequences of nest site selection

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1. Introduction

Our original aim in this project was to investigate nest site selection and its effect on the life history in a small ground nesting shorebird species the Kentish plover *Charadrius alexandrinus*. Nest site selection is an important life history decision in birds for at least two reasons. First, the concealment of the nest and eggs (e.g. by vegetation around and above the nest) may have a profound effect on nest predation, which is one of the main cause of breeding failure in birds. Second, nest microhabitat may determine the thermal conditions of the nest especially by influencing the amount of direct sunlight received, which may cause overheating. Overheating is harmful for the embryo developing in the egg and potentially fatal. Shade provided by vegetation around the nest may lessen harmful effects of sunlight. However, without shade, parental behaviour may need to be adjusted accordingly to prevent adverse effects and maintain egg temperatures near optimum. In species where both parents participate in incubation, the sexes may have different optima for nest site either because they have different incubation schedules or because they are differently affected by the environmental conditions. For example solar radiation may affect the sex more that incubates during the day, or dimorphism in plumage colouration may cause different detection probability by predators or different effect of direct sunlight on the parent.

The Kentish plover is a well suited model to investigate the life history consequences of nest site selection. This globally distributed species breeds in different locations and habitats on different continents where the amount of nest cover and ambient temperature highly vary. Nest predation is high and in some populations less than 25% of nests produce chicks. Both parents incubate the eggs and they have a markedly different schedule: males are responsible for night incubation while females do most of the daytime incubation. Males have more colourful plumage, including darker melanised colouration, that may influence their ability to incubate in direct sunlight and they can be detected easier by visual searching predators.

Our team has more than 25 years of experience of studying the breeding ecology of Kentish plovers and related *Charadrius* spp. in the field in different countries. Fieldwork methodology is standardized and used across several study sites for several decades now. This provides an exceptional opportunity to test hypotheses also across populations/species.

2. Results

During the second year of the project the COVID-19 pandemic broke out and made the planned international fieldwork impossible (or largely difficult) because of travel restrictions. During the lockdown periods we capitalized on our long-term data collected on the Kentish plover or other *Charadrius* species and investigated questions and developed and published studies related to the original aims of the proposal.

In particular we ran field studies testing questions in the project proposal (*Do birds show consistent behaviour in boldness and neohpobia tests? Are there correlations between personality traits and nest site selection? Do females or males drive nest site selection?*). Furthermore, we tested different hypotheses in relation to parental care and parental decisions on habitat selection, social interactions, brood care decisions, preen oil secretions, sex role reversal, divorce behaviour and adult sex ratios.

2.1. Landscape and climatic predictors of Kentish plover (*Charadrius alexandrinus*) distributions throughout Kazakhstan (McDonald et al. 2022, Ibis 164: 949–967)

For the breeding season in spring 2019 we planned fieldwork in West Kazakhstan where previous observations suggested high density populations of Kentish plover suitable for planned experimental tests. However, during the first three weeks of fieldwork, comprehensive surveys in West Kazakhstan failed to identify a suitably dense Kentish plover population, either at locations where high densities were previously reported or at other newly surveyed locations. To capitalise on the considerable area of West Kazakhstan sampled during Kentish plover surveys (about a 200×150 km area), we widened the scope of the survey and conducted a transcontinental survey of Kentish plover across Central Asia's largest country where information on the population sizes, breeding distributions and behaviour of shorebirds is limited. We sampled a total of 501 survey points across West, Central and East Kazakhstan between May-June 2019, and utilised species distribution modelling to outline key anthropogenic and environmental variables that determine Kentish plover presence. Our results revealed widespread distribution of Kentish plovers across Kazakhstan, but indicated that breeding densities are generally low. Our distribution modelling stresses the primary importance of proximity to water bodies and climate as the main predictors of Kentish plover presence, but reveals a weak association with indicators of human disturbance. We utilized our distribution modelling to provide the first quantitative estimate of the breeding population size of Kentish plover in Kazakhstan, which indicates a modest number of individuals given the size of the country (between 12 000 and 32 000 individuals).

This study was reported in a blogpost on the British Ornithologists' Union webpage: https://bou.org.uk/blog-mcdonald-kentish-plovers/

2.2. The impact of social structure on breeding strategies in an island bird (McDonald et al 2020, Scientific Reports 10: 13872)

Using data collected between 2007 and 2018 on pre-breeding sociality, mating decisions, nest locations, breeding dispersal and nesting success of Kentish plovers from Maio Island, Cabo Verde we investigated the impact of social structure on breeding ecology across multiple stages of reproduction with social network analysis. Sociality before breeding was connected with patterns of pair formation. In addition, site fidelity and personal breeding experience was associated with the spatial organisation of breeding pairs. Our results provided evidence that, while differential social interactions at localised scales influence patterns of reproductive pairing, site fidelity and personal breeding experience influence the structure of populations at the landscape scale. Our results underlined the tight link between the social structure of populations and patterns of mating while revealing that the relative influence of sociality, breeding experience and local ecology are dynamic across different facets of reproduction.

2.3. Remating opportunities and low costs underlie maternal desertion (McDonald et al. 2023, Evolution 77: 97–109)

Capitalizing on one of the most detailed dataset on parental care decisions in any shorebird species collected on Kentish plovers between 1996 and 1999 in southern Turkey, we investigated the costs and benefits of offspring desertion. In the Kentish plover after hatching one of the parents may leave the family (i.e. brood desertion). We firstly showed that females desert their broods more frequently than males in this population. Secondly, we investigated the benefits of this frequent female desertion in terms of additional mating opportunities, and the costs of desertion to females in terms of the growth and survival of deserted offspring. Our results indicated that female desertion is favoured by a combination of remating benefits and a lack of costs to brood growth and survival, as abandoned male parents continue to provide care after desertion. These results shed light on the costs and benefits underlying natural desertion strategies and suggest that female desertion is a fine-tuned behaviour that responds to seasonally changing benefits of desertion.

This study was featured on the HAS webpage: https://mta.hu/tudomany_hirei/a-szeki-lile-anyukaknak-megeri-elhagyni-a-csaladjukat-112718

2.4. Sex roles in parental care in a species with precocial offspring and frequent brood desertion (McDonald et al. Animal Behaviour, under revision)

Using data collected on parental behaviour of female and male Kentish plovers in southern Turkey between 1996 and 1999 we tested an important prediction of theoretical models of parental care:

task specialisation may promote biparental care as one parent is not able to provide all type of care behaviours. We firstly showed that both males and females express all care behaviours (brooding, vigilance and brood defence) characteristic of precocial species, and utilise quantitative mutual entropy analyses to show that the division of parental labour (i.e. care task specialisation) is unrelated to the maintenance of biparental care. Secondly, we showed that while males and females provide broadly similar levels of care, there are subtle differences, such that females typically deliver slightly more care than males across offspring development, suggesting that sex differences in self-maintenance may underlie sex differences in care. Together our results indicated minor differences in the care patterns of males and females, consistent with theoretical predictions that the division of labour should be limited in populations with frequent desertion and uniparental care.

2.5. Pairs show similar risk taking behaviour but only females' risk taking is linked to nest microhabitat choice in the Kentish plover (Kwanye et al. Behaviour, revision submitted)

In 2018 and 2019 in Samouco, Portugal we collected data on amount of vegetation cover above (above nest cover) and around the nest (around nest coverage), and investigated risk taking behaviour of breeding Kentish plovers using flight initiation distance (FID) as a proxy. First, we tested whether FID is repeatable. Second, we tested whether members of breeding pairs have similar FID. Third, we investigated whether male and female's FID is associated with the choice of nest microhabitat. We found that (i) FID was highly repeatable, (ii) FID was correlated within members of breeding pairs and (iii) female's risk taking behaviour was linked to the use of around nest coverage. Specifically, females with longer FID (i.e. more risk-averse ones) tended to use less concealed nest microhabitat. We concluded that nest microhabitat choice in the Kentish plovers is likely a reflection of the female's risk taking behaviour. Furthermore, breeding partners likely have similar risk taking behaviour, an indication of assortative mating.

2.6. Repeatable escape responses, but no evidence of a behavioural syndrome, in parents of a ground-nesting bird (McDonald et al. under preparation)

Similarly to the study above we collected data on risk taking behaviour of nesting plover parents on Maio Island, Cabo Verde in 2020, 2021 and 2022. Unfortunately, vegetation cover of the nests did not vary considerably in this population, thus we investigated different questions. We tested not only FIDs (boldness) but also measured the incubation recess time of individuals after FID trials in the presence of a novel object at the nest (neophobia), and investigated whether there is a correlation between these two personality measures (behavioural syndrome). This is important because, while FID responses are well characterised across species, post-FID behaviour is rarely quantified, but may have significant impacts on incubation. We collected over 200 boldness and

neophobia tests from over 70 individuals at more than 60 nests. We found a moderate but significant repeatability in FID. FIDs were also influenced by time of the day, habitat and visibility around the nest. However, incubation recess time (neophobia) was not repeatable, and the bivariate correlation between the two personality measures was weak.

2.7. Experimental investigation of nest site selection in a shorebird (Boughdiri et al. under preparation)

After two years of restrictions in doing fieldwork because of the COVID-19 pandemic, in 2022 we were able to carry out an important experiment outlined in the research proposal at the Mahres fish pond in Sfax, Tunisia. This experiment was aimed to investigate the role of males and females in nest site selection. First, we recorded incubation behaviour for at least 24h at 93 nests with different amount (0-100%) of vegetation cover over the nest. These data (after coding the over 2000 h of videos) will be used to test whether incubation behaviour of males and females is influenced by shade provided by vegetation cover. At 28 of these nests (18 with high cover and 10 with low cover) we removed one parent to captivity and distributed the eggs from the nest at other Kentish plover nests to force the other parent to remate with another mate and start a new nest. The birds placed in captivity were released after their original partner already established a new pair bond and had a new nest, and we also followed the renesting attempts of these released birds. Altogether we found the new nests of 9 females and 10 males. The incubation behaviour of the parents were recoded also at these new nests. The amount of nest cover at the new nests does not show an obvious connection with the nest cover at the original nests in either sexes, however, we need further, more detailed analyses including the behaviour data to explore all potential of this dataset.

2.8. No sex difference in the preen oil composition of Kentish Plovers during incubation (Gilles et al. under preparation)

We collected preen oil (secretion from the uropygial gland) in Samouco, Portugal in 2019 to test sex differences in the chemical composition of the preen oil during the incubation period in the Kentish plover. The samples were analysed by our collaborators at Bielefeld University, Germany. Previous works showed that sex differences in preen oil composition during incubation seem to be more common in uniparentally than in biparentally incubating species. As in the Kentish plover both sexes incubate, we predicted the absence of sex differences in preen oil composition during incubation, if preen oil indeed has a role for incubation. In the field, we sampled preen oil from 9 females and 11 males during incubation, which we analysed with gas chromatography–mass spectrometry (GC–MS). Consistent with predictions, we found no sex difference in preen oil composition, neither in beta diversity (Bray-Curtis dissimilarities) nor in alpha diversity (Shannon

index and number of substances). In Kentish plovers, the preen oil secreted during incubation may serve olfactory crypsis and protection against ectoparasites, as both functions received empirical evidence from studies on other shorebird species.

2.9. Sex role reversal and high frequency of social polyandry in the Pheasant-tailed jacana (*Hydrophasianus chirurgus*) (Fresneau et al. 2021, Frontiers in Ecology and Evolution 9: 742588)

Through a collaboration with researchers at the University of Pannonia, Hungary, data were collected on breeding behaviour of a sex-role reversed species, the pheasant-tailed jacana *Hydrophasianus chirurgus* in Taiwan in 2019. Since the very early observation of sex role reversal in this species, there was no attempt to provide a comprehensive and quantitative description of the breeding system of the species. This study aimed to fill this gap. We found that females provide most of the territory defence toward conspecifics as expected, but males also participated in agonistic behaviours. Furthermore, contrary to what was expected, we found that males spent more time than females on courtship behaviour. The polyandrous females performed mating and laying sequentially with different mates but maintained the pair bonds simultaneously with multiple males. For the first time for the species, we estimated the average number of mates per female (i.e. degree of polyandry). Finally, our observations corroborated that brood care is predominantly provided by males, nevertheless females were also participating to some degree in brood attendance but never in direct care (i.e. brooding). These results highlight that some aspects of the polyandrous breeding in the pheasant-tailed jacana deviate from the stereotyped view on sex-role reversal.

2.10. Successful breeding predicts divorce in plovers (Halimubieke et al. 2020, Scientific Reports 10: 15576)

When individuals breed more than once, parents are faced with the choice of whether to re-mate with their old partner or divorce and select a new mate. Evolutionary theory predicts that if you reproduced successfully with your partner, you should keep that partner for future reproduction. Here we investigated whether successful breeding predicts divorce using data from 14 well-monitored populations of plovers (*Charadrius* spp.). We showed that successful nesting leads to divorce, whereas nest failure leads to retaining the mate for follow-up breeding. Plovers that divorced their partners and simultaneously deserted their broods produced more offspring within a season than parents that retained their mate. Our work provides a counterpoint to theoretical expectations that divorce is triggered by low reproductive success, and supports adaptive explanations of divorce as a strategy to improve individual reproductive success.

2.11. Demographic causes of adult sex ratio variation and their consequences for parental cooperation (Eberhart-Phillips et al. 2018, Nature Communications 9: 1651)

The adult sex ratio (ASR) is a fundamental concept in population biology, sexual selection, and social evolution. However, it remains unclear which demographic processes generate ASR variation and how biases in ASR in turn affect social behaviour. In collaboration with researchers at the University of Bielefeld, Germany, we evaluated the demographic mechanisms shaping ASR and their consequences for parental cooperation using detailed survival, fecundity, and behavioural data on 6 119 individuals from six wild shorebird populations exhibiting flexible parental strategies. We showed that these closely related populations express strikingly different ASRs, despite having similar ecologies and life histories, and that ASR variation is largely driven by sex differences in the apparent survival of juveniles. Furthermore, families in populations with biased ASRs were predominantly tended by a single parent, suggesting that parental cooperation breaks down with unbalanced sex ratios. Taken together, our results indicate that sex biases emerging during early life have profound consequences for social behaviour.

3. Summary

During the project we made advances in understanding the evolution of breeding biology using Kentish plover and related species as models. These results provided notable contributions to the general knowledge of evolution of sexual and parental behaviours and were published in leading journals of the field. We also disseminated our results on national (Hungarian Ethological Society) and international (International Society for Behavioral Ecology) conferences. We produced these outputs despite the fact that the circumstances during the COVID-19 pandemic were far from ideal for the originally planned international fieldwork, however, we were fortunate to be able to utilize our long-term data to answer related questions.

Further to the scientific output, the project provided opportunity to young scientist to join our group. During the first year of the project a postdoctoral scientist G.C. McDonald joined us who was since then one of the main drivers of the project. He is now holding his own young researchers' excellence programme grant by NKFIH. A Nigerian PhD student supported by the Stipendium Hungaricum programme did the field studies for her dissertation within the framework of the project. Furthermore, the field researcher who ran the experiment in Tunisia in 2022 holds now a PhD scholarship at the University of Debrecen in the Stipendium Hungaricum programme. Additionally, we trained several local people in field biology in Kazakhstan, Cabo Verde and Tunisia.

4. Publications

4.1. Published works

Eberhart-Phillips L.J.; Küpper C.; Carmona-Isunza M.C.; Vincze O.; Zefania S.; Cruz-López M.; Kosztolányi A.; Miller T.E.X.; Barta Z.; Cuthill I.C.; Burke T.; Székely T.; Hoffman J.I.; Krüger O. 2018. Demographic causes of adult sex ratio variation and their consequences for parental cooperation. *Nature Communications* 9: 1651, DOI: 10.1038/s41467-018-03833-5

Fresneau N., Lee Y., Lee WC., Kosztolányi A., Székely T., Liker A. 2021. Sex role reversal and high frequency of social polyandry in the Pheasant-tailed jacana (*Hydrophasianus chirurgus*). *Frontiers in Ecology and Evolution* 9: 742588, DOI: 10.3389/fevo.2021.742588

Halimubieke N., Kupán K., Valdebenito J.O. , Kubelka V., Carmona-Isunza M.C., Burgas D., Catlin D., St Clair J.J.H., Cohen J., Figuerola J., Yasué M., Johnson M., Mencarelli M., Cruz-López M., Stantial M., Weston M.A., Lloyd P., Que P., Montalvo T., Bansal U., McDonald G.C., Liu Y., Kosztolányi A., Székely T. 2020. Successful breeding predicts divorce in plovers. *Scientific Reports* 10: 15576, DOI: 10.1038/s41598-020-72521-6

McDonald G.C., Bede-Fazekas Á., Ivanov A., Crecco L., Székely T., Kosztolányi A. 2022. Landscape and climatic predictors of Kentish Plover (*Charadrius alexandrinus*) distributions throughout Kazakhstan. *Ibis* 164: 949–967, DOI: 10.1111/ibi.13070

McDonald G.C., Cuthill I.C., Székely T., Kosztolányi A. 2023. Remating opportunities and low costs underlie maternal desertion. *Evolution* 77: 97–109, DOI: 10.1093/evolut/qpac020

McDonald G.C.; Engel N., Ratão S.S., Székely T., Kosztolányi A. 2020. The impact of social structure on breeding strategies in an island bird. *Scientific Reports* 10: 13872, DOI: 10.1038/s41598-020-70595-w

4.2. Submitted works

Kwanye B.Z., Barta Z., Rocha A.D., Kosztolányi A. Pairs show similar risk taking behaviour but only females' risk taking is linked to nest microhabitat choice in the Kentish plover. *Behaviour* (revision submitted)

McDonald G.C., Barta Z., Caspers B.A., Székely T., Kosztolányi A. Sex roles in parental care in a species with precocial offspring and frequent brood desertion. *Animal Behaviour* (under revision)

4.3. Works under preparation

Boughdiri H., McDonald G.C., Székely T., Kosztolányi A. Experimental investigation of nest site selection in a shorebird. Under preparation, targeted journal *Behavioral Ecology*

Gilles M., Kosztolányi A.,Rocha A, Cuthill I.C., Székely T., Caspers B.A. No sex difference in the preen oil composition of Kentish Plovers during incubation. Under preparation, targeted journal *PeerJ*

McDonald G.C., Tasman K., Engel N., Székely T., Kosztolányi A. Repeatable escape responses, but no evidence of a behavioural syndrome, in parents of a ground-nesting bird. Under preparation, targeted journal *Behavioral Ecology and Sociobiology*