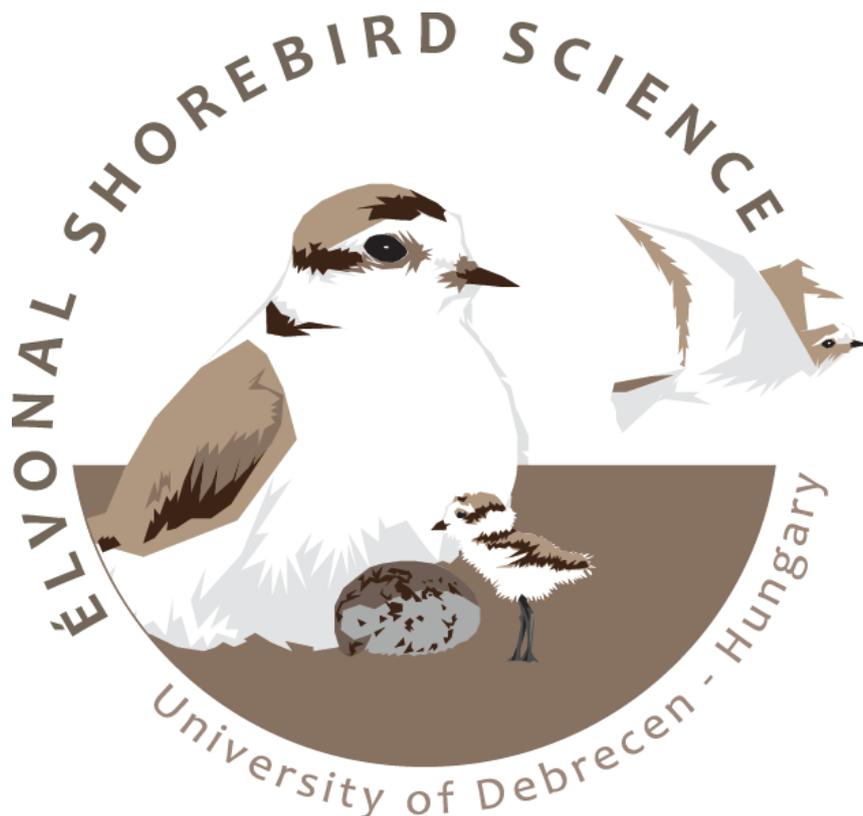


NEW DIRECTIONS IN EVOLUTIONARY RESEARCH OF SEX ROLES

10-13 January 2019, Debrecen, Hungary

Programme and abstract booklet



Organizers

Karola Szemán

Fanni Takács

Prof. Tamás Székely

Sponsors



LÁTVÁNYOS
GRAFIKAI MŰHELY



NATIONAL RESEARCH, DEVELOPMENT
AND INNOVATION OFFICE

Linguistic cooperation: Noémie Engel and Romy Rice

General information

Important phone numbers

Karola Szemán +36702568196
Fanni Takács +36203988060

Conference venue (“DAB székház”) +3652412177

Ambulance 104
Fire service 105
Police 107
Emergency number 112

Meals and social events

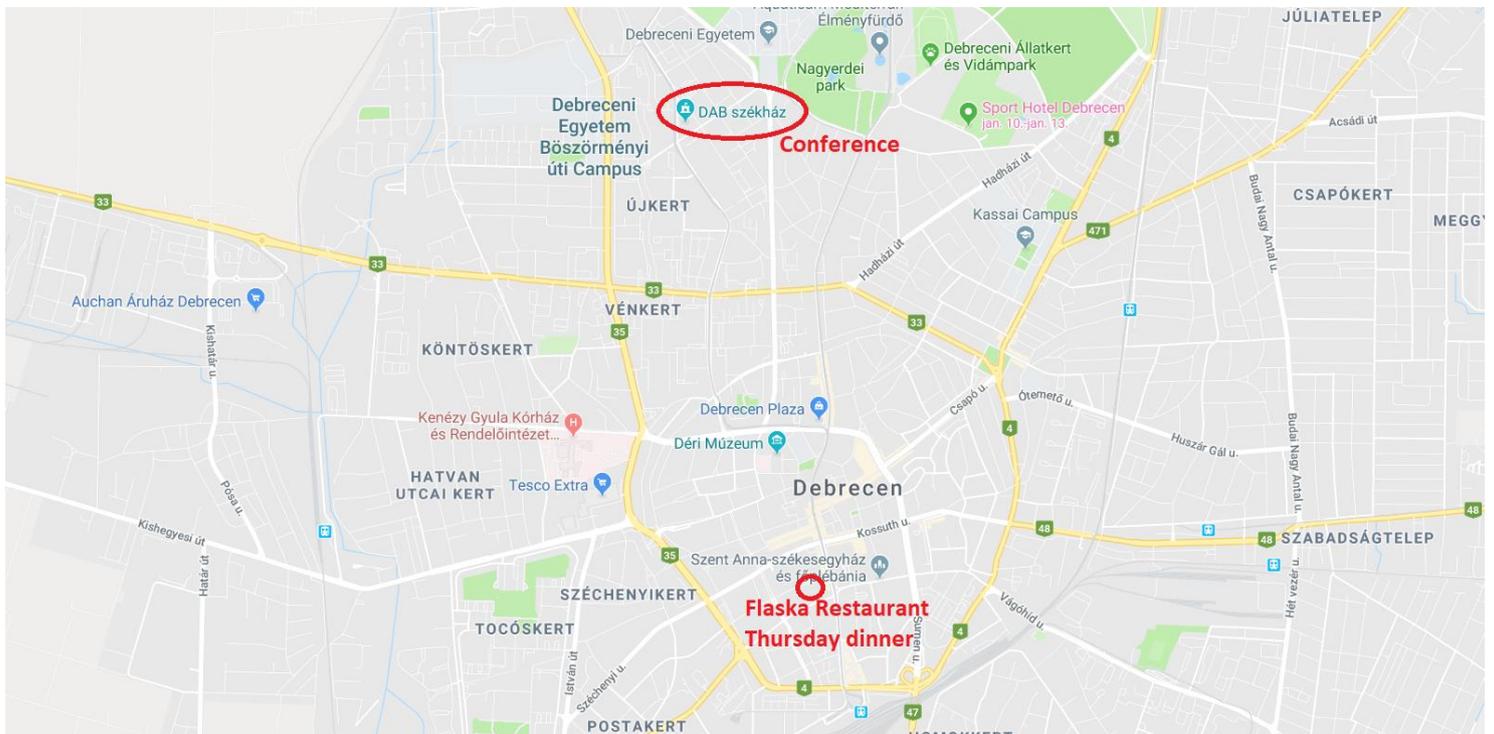
The meals are self-sponsored. The opening night will be held at Flaska Restaurant (Miklós utca. 4., Debrecen). Lunch has been booked for all participants in Melange Restaurant (Egyetem sugárút 56., Debrecen), however this is optional. Dinner is also booked for all participants on Friday and Saturday, but this is optional too. On Friday the dinner will be at Plaza Bowling (Péterfia út. 18., Debrecen) and after the dinner there will be an opportunity to go bowling and play pool. On Saturday the dinner will be at Krúdy restaurant (Medgyessy sétány, Debrecen). The cost of the two dinners is 6000 HUF in total. Due to practical reasons please have cash for upfront payment at registration. Please note, credit cards are not accepted for meals.

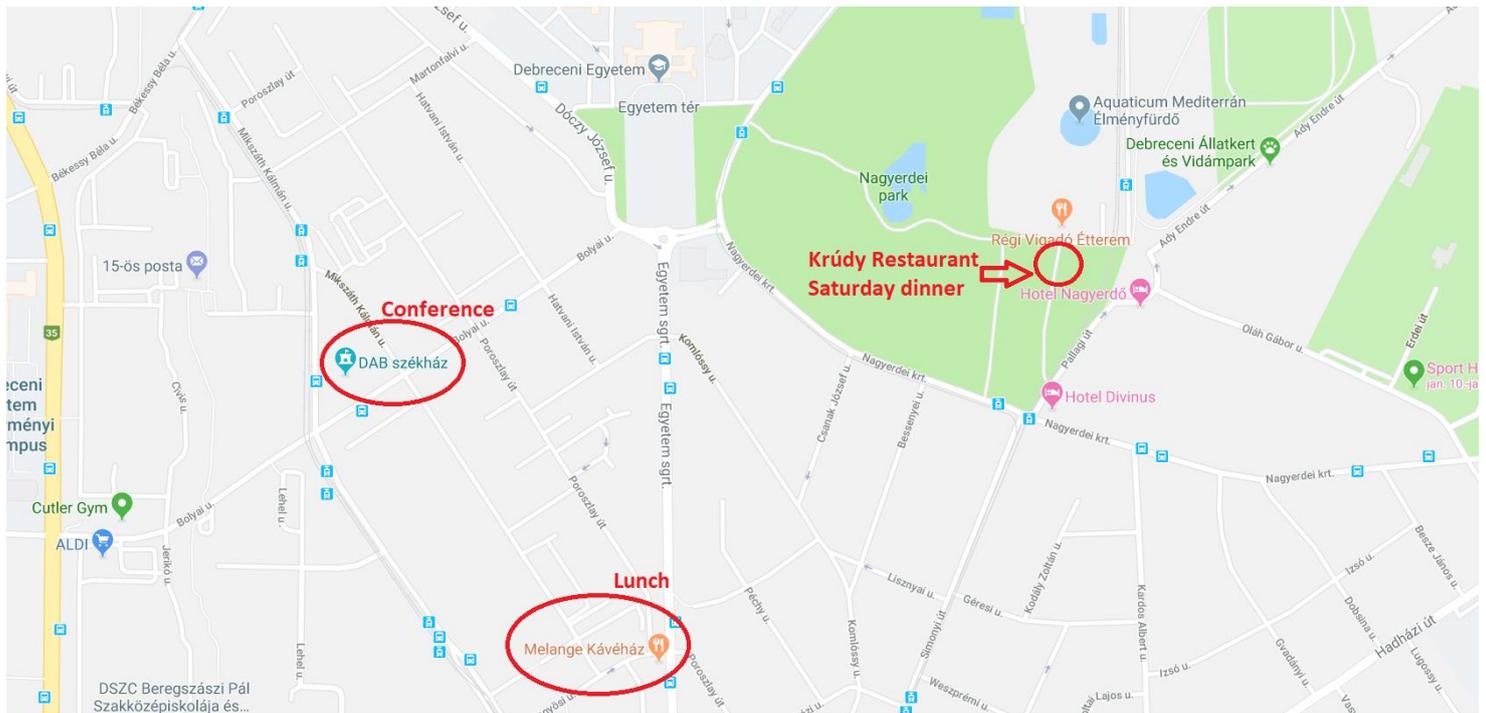
Presentation:

The format of the presentations can be PPT or PDF; however, we would like to ask everybody to have a PDF version as well as a backup.

Venue:

„DAB székház”, Thomas Mann út 49., Debrecen (first floor)





Programme

Thursday, 10th January

18:00-18:30	registration at Flaska Restaurant
18:30-19:30	Prof. Oliver Krüger The greatest adventure ever (slide show)
19:30-	dinner and social night

Friday, 11th January

8:00-8:40	registration (DAB building)
8:40-9:00	opening by Prof. Zoltán Varga
9:00-9:20	opening by Prof. Tamás Székely
<i>chair: Prof. Peter Kappeler</i>	
9:20-10:00	Dr. Elisabet Forsgren Mating competition and sex roles: what have we learnt from the two-spotted goby?
10:00-10:20	Prof. Wolfgang Goymann Males paving the way to polyandry? Parental compensation in a monogamous biparental nesting cuckoo
10:20-10:40	coffee break
<i>chair: Karola Szemán</i>	
10:40-11:20	Dr. Luc Bussiere Accounting for the extraordinary diversity of dance fly mating systems
11:20-11:40	Dr. Renata Kopena Sexual coloration of female <i>Lacerta schreiberi</i> lizards may signal health state and potential reproductive investment
11:40-12:00	Dr. Jácint Tökölyi Germline development and temperature-dependent sex change in hydra
12:00-14:00	lunch (Melange Restaurant)
<i>chair: Prof. Oliver Krüger</i>	
14:00-14:40	Dr. Claudia Fichtel Sex roles and adult sex ratios in Malagasy primates
14:40-15:00	Dr. Zitan Song Silver spoon effects of hatching order in an asynchronous hatching bird
15:00-15:20	Boglárka Morvai Sex role development in zebra finches: social effects
15:20-15:40	Jose Valdebenito The avian immune system and its possible association to sex-specific mortality
15:40-16:00	Prof. Lukáš Kratochvíl A proximate perspective on sex roles in reptiles.
16:00-16:20	coffee break
<i>chair: Dr. Natalia Karlionova</i>	
16:20-17:00	Dr. Aljeandro Serrano-Meneses The evolution of adult sex ratios in dragon- and damselflies
17:00-17:20	Prof. Ingrid Ahnesjö Examining the sex role concept, aiming for a new direction
17:20-17:40	Jia Zheng Parental care patterns are associated with the mating opportunities in Chinese penduline tits <i>Remiz consobrinus</i>
17:40-18:00	Prof. Robert Freckleton Predicting the threat status of data-deficient species
18:00-18:30	group discussion, discussion leaders: Dr. Elisabet Forsgren, Dr. Luc Bussiere
19:00-	dinner and social night (Plaza Bowling)

Saturday, 12th January

chair: Dr. Claudia Fichtel

8:30-9:10	Dr. László Zsolt Garamszegi Themes and variations in bird song at the within-individual, between-individual and between-population levels
9:10-9:40	Dr. Balázs Vági & Dr. Zsolt Végvári Abiotic and social environment predict reproductive strategies in frogs and toads
9:40-10:00	Dr. Grant McDonald The role of social and sexual networks in shaping patterns of sexual selection
10:00-10:20	coffee break

chair: Prof. Robert Freckleton

10:20-10:040	Prof. Tamás Székely Introduction to ÉLVONAL projects
10:40-11:00	Dr. Vojtěch Kubelka Associations among key components of sex roles in shorebirds
11:00-11:20	Fanni Takács Behind the scence- how do we work?
11:20-11:40	Prof. Szabolcs Lengyel Space use and alloparental care in Avocets
11:40-12:00	Ádám Kiss Conservation of Collared Pratincole (<i>Glareola pratincola</i>) in Hungary
12:00-14:00	lunch (Melange Restaurant)

chair: Fanni Takács

14:00-14:40	Dr. Liu Yang Plover studies in China: an integrated multi-disciplinary approach for studying breeding system, ecology and evolution
14:40-15:10	Dr. Natalia Karlionova Dynamics and structure of breeding waders in 2008-2018 at the Turov meadow (Pripyat floodplain, S Belarus)
15:10-15:40	Dr. Sama Zefania Comparative study of nest incubating sharing in three breeding Malagasy plover
15:40-16:00	Yuqi Wang Prolactin concentrations predict parental investment and nest survival in a free-living shorebird
16:00-16:20	coffee break

chair: Dr. Vojtech Kubelka

16:20-16:40	Naerhulan Halimubieke Mate fidelity is related to nesting success in a polygamous shorebird
16:40-17:00	Noémie Engel Incubating parents may serve as cues to visual predators in Kentish Plovers (<i>Charadrius alexandrinus</i>)
17:00-17:20	Romy Rice The breeding ecology of the Cream-coloured Courser (<i>Cursorius cursor</i>) subspecies exsul in Maio, Cape Verde
17:20-17:40	Dr. Afonso Rocha Does Adult Sex Ratio predict parental care in the Kentish Plover?
17:40-18:00	Jannik Hansen Wader breeding phenology at Zackenberg, NE Greenland – knowledge learned from 23 years of ecological monitoring
18:00-18:30	group discussion, discussion leaders: Prof. Tamás Székely, Dr. Vojtech Kubelka, Fanni Takács
19:00-	dinner and social night (Krúdy Restaurant)

Sunday, 13th January

8:00-23:00	Optional excursion to Hortobágy National Park, and dinner & wine tasting in Tokaj region
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Abstracts

Examining the sex role concept, aiming for a new direction

Ingrid Ahnesjö¹ and Malin Ah-King²

¹ *Uppsala University*, ² *Stockholm University*

The concept of “reversed sex-roles” has made us explore the diversity in mating competition and parental care among animals. Both mating competition and parental care are often intimately linked to the process of sexual selection. We increasingly view the process of sexual selection as equally relevant in both males and females and to act in similar ways in both sexes. So why do we divide species into sex-role reversed or not? This is often done in relation to a common pattern (or norm) of, for instance, that males compete for matings and females care for offspring. Consequently, the sex-role concept carries a dichotomy with typological arguments that needs to be examined. It is now time to discuss how we can go beyond the sex-role concept, to better understand diversity and dynamics in what sexes are selected to do under the influence of ecological factors.

Accounting for the extraordinary diversity of dance fly mating systems

Luc F. Bussière¹

¹*University of Stirling*

Even when sexual selection on females is strong, female ornaments are rare and typically modest (at least in contrast to extravagant male traits in highly dimorphic species), perhaps because males should rarely prefer mates that divert resources away from offspring to expensive displays. Preferences for female ornaments are even harder to explain if attractive females present a higher risk or intensity of sperm competition (e.g., because they mate more often): in such cases, the most adorned females should be avoided rather than preferred, since their mates would otherwise have to share paternity with a larger group of competitors.

Notwithstanding these constraints, female dance flies (Diptera: Empididae: Empidinae) exhibit tremendous (and as-yet unexplained) diversity in the presence and intensity of ornament expression, including some of the most spectacular adornments in the animal kingdom. In my seminar I will present an overview of the group's remarkable range of behaviour and morphology, describing the typical ritualized transfer of "nuptial gifts" from males to females during courtship and its role in shaping diversity in sexual receptivity, polyandry, mate choice and sexual conflict. I will also present new work quantifying selection and coevolution between female and male characters, and explain its implications for recent claims about the symmetry of selection in species with stereotypical and atypical sex roles. I will argue that sharply contrasting constraints on selection for male and female life histories help to shape the exceptional diversity of dance flies, and offer lessons on the nature of selection for mating system diversity across the animal kingdom.

Incubating parents may serve as cues to visual predators in Kentish Plovers (*Charadrius alexandrinus*)

Noémie Engel¹, Romy Rice¹, Zsolt Végvari¹, Tamas Székely²

¹*Department of Evolutionary Zoology and Human Biology, University of Debrecen, Hungary.*

²*Milner Centre for Evolution, Department of Biology and Biochemistry, University of Bath, UK.*

Shorebirds face many challenges when trying to reproduce with nest predation being the main cause of reproductive failure. Focusing on visual predation mechanisms, this study aimed to elucidate what cues are used by visual predators to locate their prey. With the Kentish plover (*Charadrius alexandrinus*) as study model, experimental tests mimicking male and female incubating adults on the island of Maio, Cape Verde, indicated that incubating parents may predict nest mortalities and therefore serve as cues to predators. No difference was found in predation rates between sexes ($p=0.737$). Several layers of evidence such as camera evidence, tracks and marks revealed that it was mainly brown-necked ravens (*Corvus ruficollis*) that visually predated the incubating parents. Survival rates differed between three distinct experimental zones with the ones in a shrubby, grassy habitat surviving best, potentially due to better protection with vegetation cover. With only 23.5% of nests having hatched in 2015 and 2016 in Maio, the Kentish plover is vulnerable and faces changes of population structure. The newly obtained evidence can be used in future projects as a tool to improve hatching success. It may contribute to the design of novel conservation strategies testing targeted anti-predator actions that may result in increased nest survival and a vigorous breeding population.

Sex roles and adult sex ratios in Malagasy primates

Claudia Fichtel¹ and Peter Kappeler¹

¹*German Primate Center, Göttingen*

In virtually all sexually reproducing species, males and females differ in the degree of within-sex reproductive competition, how discriminating individuals are during pair formation and the extent to which they exhibit parental care after mating. These sex roles have been thought to be related to how much males and females invest in gamete production, but recent research has indicated that a species' life history and the ratio of males and females in a population – the adult sex ratio (ASR) – can be more important determinants of interspecific variation in sex roles. The primates of Madagascar (lemurs) are interesting in this context because they evolved components of sex roles that deviate from the traditional patterns known from most other primates, including female dominance over males. We use long-term demographic and behavioral data to examine the relationship between sex roles and ASR in Verreaux's sifakas (*Propithecus verreauxi*). In particular, we focus on the causes and behavioral consequences of the unusual male-biased ASR, showing, among other effects, how mortality rates differ between the sexes and that male natal dispersal is guided by local variation in ASR. Thus, focusing on ASR may provide a promising approach towards explaining the unusual sex roles in this primate radiation.

Mating competition and sex roles: what have we learnt from the two-spotted goby?

Elisabet Forsgren¹ and Trond Amundsen²

¹Norwegian Institute for Nature Research, Trondheim, ²Norwegian University of Science and Technology

In most animals, mating competition is strong among males and they compete over females, while females are less eager to mate. However, in some species the opposite is true, and in yet others it varies. Our understanding of sexual selection has greatly improved during the last decades and the focus is no longer solely on males, but also on female competition and male mate choice. Understanding what controls the strength of mating competition is key in our understanding of sexual selection and animal mating systems. Several factors have been suggested to affect the strength of mating competition, one of these being the operational sex ratio (OSR; the ratio of males and females ready to mate). The two-spotted goby, *Pomatoschistus flavescens* (formerly *Gobiusculus flavescens*), a small semi-pelagic fish with paternal care, has turned out to be a good model for investigating what controls mating competition and related questions. Here, some of the main results from our studies on this species will be presented. A well-studied Swedish population demonstrated exceptional temporal variation in OSR and mating competition. In the beginning of the season males competed over matings while females became the more competitive sex later in the season. Hence, sex roles are dynamic, changing from conventional to role-reversed. This followed a change in the OSR from male biased to strongly female biased over the breeding season. Lab experiments confirmed that OSR affects mating competition and the opportunity for selection. The variable sexual selection regime in the species likely explains why both male and females have ornamental colours. Moreover, field observations of mate sampling females showed seasonal changes in behaviours related to mate choice and choosiness of both sexes. Lastly, recent findings in a population further north (mid-Norway) reveal striking spatiotemporal variation in OSR and mating competition between the populations. This can likely be explained by differences in climate and associated female life history tactics.

Predicting the threat status of data-deficient species

Robert Freckleton¹

¹University of Sheffield

Comparative methods have conventionally been thought of as correlative approaches based on observational data. However, the models we fit to comparative data are evolutionarily informed (i.e. based on mechanisms), and therefore should be capable of being used predictively. We have used these models (combining space and phylogeny with independent explanatory variables) to model and predict the threat status of data deficient species. Here I describe the application of this approach to birds and amphibians.

Themes and variations in bird song at the within-individual, between-individual and between-population levels

László Zsolt Garamszegi¹

¹ *Estación Biológica de Doñana-CSIC*

Bird song is known as the acoustic analogue of the peacock's tail, and is often used as a model in sexual selection studies. Most research has focused on between-individual differences in song traits and investigated questions about how aspects of male quality can be signalled and how these can be translated into fitness benefits. However, bird song is a very special in a sense that it can also show a considerable variation within individuals, while spatio-temporal patterns define biologically important patterns of variations at the between-population level. My research group has been studying the song of the collared flycatcher (*Ficedula albicollis*), which has a modestly complex system with males using 15-50 different syllable types in their individual-specific repertoires that they vary with high plasticity. In our earlier studies, by adopting the classical focus from behavioural ecology on between-individual variations, we determined the information content of male repertoires its relationship with mating success. More recently, we investigate how songs change within individuals across different temporal windows (within- and between days, and between years) and how such reaction norms differ among individuals and what are the fitness consequences of this variation. At a higher level, we study compositional changes in song at the between-population level, which open horizons for understanding the dynamics of cultural evolution. In my talk, I will provide examples from our model species to demonstrate the evolutionary relevance of the complex hierarchical organization of bird song.

Males paving the way to polyandry? Parental compensation in a monogamous biparental nesting cuckoo

Prof. Wolfgang Goymann¹

¹ *Max-Planck-Institut fuer Ornithologie*

Social monogamy in combination with biparental care is the most common breeding system of birds. Why this is so is still not well understood. I studied the importance of female and male contributions to offspring care in white-browed coucals (*Centropus superciliosus*), which belong to a group of nesting cuckoos and are monogamous and biparental. Females, however, occasionally become polyandrous – presumably when a surplus of males becomes available – and may nest with an additional male. In these cases, the secondary males raise their offspring without or with only little help from the female. To study the effect of female and male contributions to care in white-browed coucals I conducted a removal experiment, during which one partner was temporarily removed for 3 days to see whether the remaining parent compensates for the loss of the removed parent. Both female and male white-browed coucals approximately doubled their feeding rates when their partner was removed, thus fully compensating the number of feeding visits to the nest. However, the growth rate of nestlings was maintained only upon female removal. When the male was removed nestling growth declined. Hence, only male white-browed coucals can fully compensate the loss of the partner. This suggests that females may benefit from nesting with additional males, if these should become available, and that the monogamous breeding system of white-browed coucals is maintained because of a relatively balanced sex ratio.

Mate fidelity is related to nesting success in a polygamous shorebird

Naerhulan Halimubieke¹, J. O. Valdebenito¹, P. Harding, M. Cruz-López², M. A. Serrano-Meneses³, R. James¹, K. Kupán⁴, T. Székely^{1,4}

¹University of Bath, ²Universidad de Guanajuato, ³Universidad de las Americas Puebla, ⁴Eötvös Lóránd University, ⁵University of Debrecen

Mate choice and pair bonding play important roles in the evolution of breeding systems. Retaining or divorcing a mate can have a substantial impact on the reproductive success, especially in populations that breed multiple times within a year. Here, we investigate mate retention in a polygamous shorebird, the Snowy Plover (*Charadrius nivosus*), in which both males and females may have several breeding attempts within a breeding season by keeping their mate or divorcing from them. By using six years of data from a well-monitored population in Bahía de Ceuta, Mexico, we investigate potential predictors of mate fidelity both within and between years. We show that successful nesting leads to divorce in the same year, and thus divorced plovers – counterintuitively – achieve higher reproductive success than individuals that retain their mate. We also show that mate fidelity is driven by different factors within- and between-years. Taken together, understanding mate fidelity is important for endangered birds like the Snowy Plover given the implications of divorce for reproductive success, adult survival and population productivity.

Wader breeding phenology at Zackenberg, NE Greenland – knowledge learned from 23 years of ecological monitoring

Jannik Hansen¹

¹*Aarhus University*

In the Zackenberg Valley, Northeast Greenland, a monitoring programme was set up in 1996, trying to monitor an entire ecosystem; or most of one. Weather, snow melt, permafrost, gas exchange, plants, insects, mammals, birds, fish etc. Part of the programme works with waders, and one area of monitoring is the breeding phenology of waders. We have three target species; the sanderling, the dunlin and the ruddy turnstone. Over the 23 seasons we have followed these birds, we have learned that inter-annual variation is considerable, and pictures really do not emerge before quite some years of data have been collected. While other monitoring subjects have made a change towards earlier flowering and emergence (insects), the birds breeding phenology seem to be less plastic in the early part of the season. There has been very little change. The variation between years is mainly seen as delays on snow rich years and those with late snow melt. Inter species variation is chiefly down to habitat choice; turnstones often breeding on poorly vegetated areas such as ridges and other early snow free areas, sanderlings on heath and hill sides, and finally, dunlin in fens. In the future, we would like to get projects to supplement the monitoring with more detailed studies.

Dynamics and structure of breeding waders in 2008-2018 at the Turov meadow (Pripyat floodplain, S Belarus)

Yauheniya Luchy¹, Natalia Karlionova¹, Viachaslau Khursanau¹

¹*Scientific-practical Centre for bioresources NAS Belarus*

The Pripyat floodplain supports significant breeding populations of waders commonly associated with lowland grasslands such as Northern Lapwing (*Vanellus vanellus*), Redshank (*Tringa tetanus*), Black-tailed Godwit (*Limosa limosa*), and Great Snipe (*Gallinago media*). More than 70% of the Belarusian population of Common Ringed Plover *Charadrius hiaticula* and Terek Sandpiper *Xenus cinereus* breed on the flooded meadows of the Pripyat.

From 2008 we started breeding waders monitoring in the Pripyat floodplain meadows on territory of "Turov Meadow" reserve. We recorded all wader nests and birds with breeding behavior in a 140 ha study area near Turov town, Gomel Region (52.04°N, 27.44°E).

Up to 13 species of waders and more than 20 species of other waterbirds breed on this territory every year.

The main reasons for the decline of breeding density of wader local populations in the floodplain of the Pripyat River were as follows:

- the overgrowing of meadows by willow shrubs;
- the low water level;
- the high level of predators' pressure.

For last decades total numbers of the 13 breeding wader species recorded decreased significantly ($R^2=0.55$, $p<0.05$). Similarly three individual species had negative population trends: Northern Lapwing, Common Ringed Plover and Redshank.

In 2018 we recorded 427 pairs of 12 wader species breeding within the project area "Turov meadow", which is twice as large as in 2013. The number of Lapwings was 185 breeding pairs, Redshanks - 164 breeding pairs, a Black-tailed godwit - 38 breeding pairs, which is 2-4 times higher than the number in previous years. The density of the nests on the breeding area of the meadow varied between 130 and 2 pairs per hectare. The overall breeding success of waders was 88%.

As a result, a complex of biotechnical measures allows to preserve this territory in the most favorable condition for breeding waders. A high level of water in the river provided the presence of large colonies of terns and gulls, which actively protect their nesting areas from predators and at the same time make breeding conditions more safe for waders.

Conservation of Collared Pratincole (*Glareola pratincola*) in Hungary

Ádám Kiss¹, Ákos Monoki¹, Antal Széll¹

¹*Hortobágy National Park*

The Collared Pratincole (*Glareola pratincola*) is a critically endangered and strictly protected bird species in Hungary. Until the late 1980s, this bird was a characteristic breeder in alkali steppes. In modern times, its population almost totally disappeared from the region. The present Hungarian population harbours 35-50 nesting pairs. In parallel to decreasing population size, the species disappeared from its traditional nesting sites. Currently, Collared Pratincoles nest almost exclusively in agricultural areas. Species protection is challenged by several factors. Here I outline management techniques and a long term management plan of the Collared Pratincole to be applied in Hungarian national parks

A székicsér kritikusan veszélyeztetett, fokozottan védett partimadár-faj Magyarországon. Az 1980-as évek végéig az alföldi szikesek jellegzetes fészkelője volt, mára állománya szinte teljesen felmorzsolódott. Jelenleg a hazai populáció nagysága 35-50 pár között mozog. Állománycsökkenéssel párhuzamosan a faj tradicionálisnak számító szikespusztai fészkelőhelyeiről teljesen eltűnt és szinte kizárólag szántóföldi környezetben költ. Védelmét számos környezeti tényező nehezíti. Gyakorlati védelmét és a faj hosszútávú megőrzését az előadásban jellemzett módszerek alapján végzik az érintett nemzeti park igazgatóságok szakemberei.

Sexual coloration of female *Lacerta schreiberi* lizards may signal health state and potential reproductive investment

Renata Kopena¹, Pilar López², Viktoria Majlathova³ and José Martín⁴

¹*Eötvös Lóránd University*, ²*Museo Nacional de Ciencias Naturales Madrid Spain*, ³*Slovak Academy of Sciences*,
⁴*Spanish National Research Council*

Female animals often have conspicuous, or less conspicuous but well-recognizable by conspecifics, sexual ornaments, but their evolution and function are less-known than those of males. Female ornaments can evolve and be maintained as a result of a non-adaptive process of intersexual genetic correlation between males and females, but these traits can also indicate female quality, informing, for example, about the strength of the immune system, parasite burden and condition or potential fecundity and investment into offspring. We examined whether pigmental or structural-based coloration of female Spanish green lizards (*Lacerta schreiberi*) may function signaling their condition, parasite infections and strength of immune response and whether these features can predict their potential reproductive investment. We found that females with longer body sizes had stronger PHA-induced immune responses and relative clutch size had negative effect on condition of mothers after egg laying. Different parasite infections influenced female coloration differently. Mother coloration may predict several components of reproductive investment, such as incubation time, hatching success, and size and condition of their hatchlings. These indicator signals support direct sexual selection of female ornaments. However, due to the similar basis of coloration in both gender, genetic correlation is neither excluded. Moreover, these two phenomena would increase even synergistically the fitness of individuals that prefer these color signals.

A proximate perspective on sex roles in reptiles

Lukáš Kratochvíl¹

¹*Charles University*

Reptiles are a highly diversified vertebrate group with extensive variability in social behaviour and sexual dimorphism. This variability is rather surprising as many sexually dimorphic traits are believed to be under control of male gonadal androgens. During last years, we investigated the hormonal control of male sexual behaviour, male aggressiveness, cues responsible for sex recognition and sexual dimorphism in geckos and other lizards based on hormonal manipulations. We found that male sexual behaviour is indeed controlled by male gonadal androgens. However, longer exposure to circulating androgens is needed for the onset of male sexual behaviour, which can continue for a long time after the levels of these hormones drop. We suggest that this observation can parsimoniously explain several earlier discrepancies and debatable conclusions on the apparent variability in the hormonal control of male sexual behaviour in vertebrates, which were based on behavioural testing at a few subjectively selected time points. Our results point that male aggressive behaviour and development of hemipenes are controlled by male gonadal androgens, but only indirectly, as the metabolization of circulating androgens to estrogens seems to be required. On the other hand, estrogens are not necessary for female sexual attractiveness and recognition of an individual as a female. The sex recognition cues are likely directly masculinized by male gonadal androgens. We also demonstrated that sexually dimorphic growth is not controlled by male gonadal androgens, but by ovarian hormones. Overall, it appears that individual behavioural and morphological sexually-dimorphic traits are controlled by multiple endogenous pathways, which could have permitted their disentangling during evolution and the occurrence of (semi)independent changes across phylogeny.

Associations among key components of sex roles in shorebirds

Vojtěch Kubelka¹, Fanni Takács¹ & Tamás Székely^{1,2}

¹*University of Debrecen, Hungary,* ²*University of Bath, United Kingdom*

Within the new cross-disciplinary project, ÉLVONAL SHOREBIRD SCIENCE (<https://elvonalshorebirds.com/>) that uses behavioural ecology, population demography, comparative genomics, theoretical modelling and shorebirds as an excellent model system, the first objective is targeting the investigation of core components in sex roles variation.

To understand the fundamental associations among key components of sex roles: courtship, pair bonding, incubation and parental care, we are investigating several populations of shorebird species worldwide with help of many collaborators.

During the presentation, we will provide a short overview of the current cooperation and then we will discuss in detail the prepared fieldwork protocol for behavioural observations (courtship and parental care) as well as methodologies how to quantify best the parental contribution to incubation and how to monitor pair bonding. Following colour-marked individuals preferably over several breeding seasons is essential within this project.

We are looking forward to discuss and update the fieldwork protocol together with our collaborators as well as we are happy to discuss the new prospective cooperation with dedicated researchers enthusiastic about shorebirds.

Space use and alloparental care in Avocets

Prof. Szabolcs Lengyel¹

¹*Hungarian Academy of Sciences, Centre for Ecological Research*

In this talk I use observational and experimental data from a four-year field study to provide spatial explanations for the phenomenon of chick adoption in Pied Avocets (*Recurvirostra avosetta*). Avocets in south-central Hungary typically nest in colonies on islands that emerge from shallow soda lakes. Nests in colonies are usually synchronous, which allows synchronous hatching of the chicks. As a result, most of the chick adoption events occur in the nesting colony. Pairs with young chicks leave the colony and move to feeding areas and some adoptions also occur during these brood movements. The brood movements are costly in terms of chick survival due to high predation in artificial habitats and less so in natural habitats. Chick adoption was associated with higher survival of the parents' own young probably due to a dilution of the effects of predation. Laying more eggs could thus provide fitness benefits in the face of high predation. However, results of a brood manipulation experiment showed that Avocets, as almost all shorebirds, cannot lay more eggs than their fixed clutch size of four due to the high costs of incubating larger-than-normal clutches. My results suggest that patterns and processes in alloparental care in birds with precocial young cannot be fully understood without proper knowledge of variation in habitat quality and space use by the birds.

Plover studies in China: an integrated multi-disciplinary approach for studying breeding system, ecology and evolution

Yang Liu¹, Pinjia Que², Chung-Yu Chiang³, Eben Goodale⁴, Araxi O. Urrutia⁵, Zhengwang Zhang², Tamás Székely⁵

¹*Sun Yat-sen University*, ²*Beijing Normal University*, ³*Tunhai University*, ⁴*Guangxi University*, ⁵*University of Bath*

The Kentish Plover (*Charadrius alexandrinus*) is a geographically widely distributed species that occurs in North Africa, Europe, Central Asia and East Asia. In China, populations breed on coastlines, inland saline lakes and islands crossing different climatic zones from temperate areas to tropics, and spanning from lowland habitats to Tibetan Plateau. Thus this system provides ample opportunities to understand speciation, breeding system evolution, local adaptation and conservation. Geographical variations in morphology, population ecology, behaviors and genetics have been intensively investigating among populations in Chinese Kentish Plovers by Chinese researchers through international collaboration. In my talk, I will review recent progress on plover studies in China and discuss about future perspective.

Vocal response of male serin, *Serinus serinus*, to interactive playback

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Song overlapping and alternating in birds has been studied over the past few decades and spawned some controversy over its communicative value. Proposed hypotheses to explain the function of this vocal behavior leads to quality and/or motivation signaling. Results of previous experiments showed that male serin react to songs with shorter inter-syllable intervals but not to frequency variations. We analyze vocal response to interactive playback attempting to rate alternate and overlap song stimuli influence. Analyzing overall differences in responses between experimental treatments, namely song length and interval between songs and syllables, we found a decrease in male song length with playback overlapping and alternating. The results suggest that singing in overlap and alternate can be considered a threat but male reaction is different. Decrease in syllable rate point out that males slowed their songs. Temporal variations and song timing occurred during playbacks appear to be related to a form of preventing overlapping (Poop et al. 1985, Naguib and Mennill 2010). This results show that there may be a conflict avoiding or a way of trying to reduce level of aggression.

The role of social and sexual networks in shaping patterns of sexual selection

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Research indicates that animal populations are characterised by non-random social structure. This structure emerges from systematic variation in interactions between individuals as consequence of behavioural, environmental and demographic processes. Social structure can have important fitness consequences for individuals by influencing access to resources, cooperative behaviours, and the spread of information and disease. Recent work suggests that this structure can also have implications for intrasexual competition and the intensity of sexual harassment. Understanding the implications of complex patterns of social and sexual interactions for the evolution of male and female reproductive strategies requires methodologies to characterise this structure. Here, we use network analysis to characterise the structure of social and sexual interactions in simulated populations and experimental groups of polygynandrous red junglefowl (*Gallus gallus*). We show that (i) the structure of sexual networks has strong implications for the strength sexual selection on males and (ii) the structure of sexual networks is underpinned by differential female sociality. Collectively, these results indicate that sexual networks influence the strength of sexual selection and reveal female sociality as a force governing the landscape of intra-sexual competition and the emergent structure of animal societies.

Sex role development in zebra finches: social effects

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How are sex roles transferred between generations? Previous research has mainly focused on genetic mechanisms, despite of the well-established role of social learning in other sex role related behaviours (i.e. sexual imprinting, mate choice copying). Here we investigated whether nestlings of a socially monogamous, biparental passerine, the zebra finch (*Taeniopygia guttata*) learn sex roles socially. We used two experimental approaches: split-family design and cross-fostering, to manipulate parental care and faithfulness experienced by nestlings. We found that incubation patterns of first breeding uniparentally-raised zebra finches were influenced by which of their parent took care for them and their partner, however, we found no effect at later reproductive stages (during offspring provisioning) and during the second breeding. Furthermore, nestlings raised by two foster parents showed parental and extra-pair behaviours similar to their genetic parents. We concluded that early social experiences (or the lack of them) from parents can result in a disrupted parental sex role division, although these effects are not persistent and „normal” sex role patterns can be assumed based on interactions with the partner. Our results suggest that genetic rather than social inheritance is responsible for the trans-generation transmission of parental care and faithfulness behaviour.

The breeding ecology of the Cream-coloured Courser (*Cursorius cursor*) subspecies *exsul* in Maio, Cape Verde

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The Cream-coloured Courser (*Cursorius cursor*) subspecies *exsul* is an endangered wader endemic to the Cape Verde archipelago. Very little is known about this bird, with major gaps in its biology, behaviour and breeding ecology. We studied the breeding ecology of the resident population occupying the island of Maio during three consecutive breeding seasons (2015 – 2017). We found a total of 40 nests, the majority of them located in the Salina do Porto Inglês, the largest wetland area of Maio. Clutch size was consistent, always with 2 eggs per nest. Hatching success was high, with approximately 43% of nests producing at least one chick. Finally, parental care seemed to be bi-parental, with male and female providing an equal amount of care. Further research is required to increase understanding of the parental sex-roles.

Does Adult Sex Ratio predict parental care in the Kentish Plover?

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Sex role reversal is characterized by higher female intrasexual competition and male parental care. The mechanisms for sex role reversal remains poorly understood. Adult sex ratio (ASR), defined as the number of adult males to adult females in the population, is becoming increasingly recognized as an important predictor in mating systems and parental care.

ASR affects sex roles by influencing mating opportunities. Female-biased ASR tends to conserve conventional sex roles, while male-biased adult sex ratio is associated with sex role reversal. While being well-tested empirically, the implications of ASR on wild populations remain vastly understudied. The Kentish Plover (*Charadrius alexandrinus*), is a highly appropriate model organism for this purpose, given the unusual flexibility in its mating and parental care systems. This study analyses the effects of ASR on parental care in the Kentish Plover, using incubation behaviour as a measure of parental care, alongside variables that are known to affect avian incubation: ambient temperature, julian day and incubated days. ASR did not predict incubation behaviour; the only variable that had a significant effect on incubation behaviour was incubated days. The results of this study emphasize that ASR alone is not sufficient to determine incubation behaviour, as it is a behaviour that is influenced by many confounding factors. Higher resolution of data, especially ASR survey data, is required for a more conclusive study.

The evolution of adult sex ratios in dragon- and damselflies

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Adult sex ratio (ASR), the proportion of adult males to adult females in a population, has important effects on behaviour, population dynamics and ecology. ASR can vary dramatically; sometimes, even amongst the populations of a single species. Nonetheless, the underlying causes of ASR variation in the vast majority of taxa remain obscure. In this study, we used phylogenetic comparative methods to investigate whether behavioural (mating system) and morphological traits (body size, sexual size dimorphism, and male wing pigmentation) may bias ASRs in dragon- and damselflies (Insecta: Odonata). Our results show that (i) dragonflies exhibit ASRs closer to unity, whereas in damselflies, more male-biased ASRs are prevalent, and (ii) a significant interaction term mating system*body size suggests that in non-territorial odonates, evolutionary increases in body size correlate with evolutionary increases in female-biased ASR. The latter result is likely, since the males of non-territorial taxa actively search for females and exhibit similar body sizes to females. Small male body size may be energetically more advantageous to the males of these taxa. We suggest that larger-than-average males may experience lower survival, given the higher costs of large body size, thereby shaping the observed pattern of ASR in non-territorial taxa.

Silver spoon effects of hatching order in an asynchronous hatching bird

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The silver spoon hypothesis proposes that individuals which develop under favourable conditions will gain fitness benefits throughout their lifetime. Hatching order may create a considerable size hierarchy within a brood and lead to earlier-hatched nestlings having a competitive advantage over their siblings, which has been illustrated in some studies. However, there have been few explorations into the effect on subsequent generations. Here, using a 15-year-long study, we investigated the long-term fitness consequence of hatching order in the endangered crested ibis, *Nipponia nippon*, a species with complete hatching asynchrony. In this study, we found strong support for silver spoon effects acting on hatching order. Compared to later-hatched nestlings, first-hatched nestlings begin reproduction at an earlier age, have higher adult survival rates, possess a longer breeding life span and achieve higher lifetime reproductive success. Interestingly, we found carry-over effects of hatching order into the next generation. Nestlings which hatched earlier and became breeders in turn also produced nestlings with larger tarsus and better body condition. Additionally, we found a positive correlation among life-history traits in crested ibis. Individuals which started reproduction at a younger age were shown to possess a longer breeding life span. And the annual brood size increased with an individual's breeding life span. This suggests that the earlier-hatched nestlings are of better quality and the 'silver spoon' effects of hatching order cover all life-history stages and next generation effects.

Introduction to the ÉLVONAL project

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Sex roles are some of the most diverse social behaviour, since courtship, pair-bonding and parenting exhibit immense variation between and within species. My research group has made major contribution to sex role research although significant issues remained to be resolved. We are focusing on shorebirds - an avian taxa that exhibit an unusually diverse sex role behaviour. Recently we showed that a significant - but somehow neglected - aspect of sex role evolution is adult sex ratio (ASR, proportion of males in the adult population), a demographic property of populations - since the more abundant sex in the population has more mating options than the rarer sex. We also showed that sexual selection instead of being an engine of speciation as commonly thought, it slows down diversification.

This ÉLVONAL project synthesises research and fill major knowledge gaps. This is a cross-disciplinary project that uses behavioural ecology, population demography, comparative genomics and theoretical modelling to investigate the causes and implications of sex role variation. By building upon decades of skills, experience and knowledge in various shorebirds, we propose to carry out experimental, demographic and genomic projects to separate the roles of ecological and demographic processes on sex roles. This is an ambitious project that has the potential to go beyond state-of-the-art in sex role research, and it will propose future directions for this research field.

Germline development and temperature-dependent sex change in hydra

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Freshwater cnidarians of the genus *Hydra* have diverse reproductive strategies with both hermaphroditism and gonochorism (i.e. separate sexes) occurring in different species. Sex in this system is determined at the level of the stem cells and interactions between these cells shape reproductive investment and sex allocation. *Hydra oligactis* has separate sexes that are thought to be relatively stable, with low rates of sex change. However, population genetic data indicates that sex change might be more common under field conditions. To investigate sex change under ecologically relevant conditions, I exposed hydra polyps from a male and female *H. oligactis* strain to temperature fluctuations simulating seasonal changes in temperature (7 to 18 °C) and quantified sexual propensity and sex ratio. Sexual reproduction was lacking in polyps kept continuously on 7 °C. A short exposure (1 week) to elevated temperature resulted in a very small proportion of polyps initiating sex. A longer exposure (8 weeks) to 18 °C substantially increased the proportion of sexual polyps. However, about half of these animals had different sex than their parental strain, indicating substantial sex change. These results indicate that exposure to elevated temperatures is required in this species for germline development. Germlines derived from somatic tissue have unstable sex and therefore sex change is likely to be very common under field conditions. The ultimate factors behind sex change in hydra are still to be understood.

The avian immune system and its possible association to sex-specific mortality

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Sex-specific mortality is frequent in animals although the causes of sex differences in mortality remain poorly understood. Parasitism has a ubiquitous presence in nature with mortality implications, and a previous study in mammals found that sex difference in parasite prevalences predicted sex-specific mortality. Using sex-specific blood and gastrointestinal parasitism data and annual mortality from 149 bird species that represent XX avian orders, here we test whether parasitism predict sex-biased mortality in adult birds using phylogenetic analyses. We found no difference in parasite prevalence of adult males and females, although importantly, blood parasite prevalences increased with body mass of males and females. Nevertheless, there was no correlation between sex-biased mortalities and sex-biased parasite prevalence. These results were consistent in both blood and gastrointestinal parasites. Taken together, we confirm that body size is an important predictor of blood parasitism, although in birds – unlike in mammals – parasite prevalences are not different between adult males and females. We propose that more complex models incorporating the impact of predation or immune capacity may be necessary to explain sex-biased mortality.

Abiotic and social environment predict reproductive strategies in frogs and toads

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Amphibians exhibit unusually diverse reproductive modes including paternal care strategies. Understanding the drivers of this variation is important given that this group included the first vertebrates that bred in terrestrial environments. Using phylogenetic analyses of over 1000 species of frogs and toads (Anura), we investigate correlational and causal associations among sex-specific modes of nest building and offspring protection, territory defence and climatic characteristics (ie ambient temperature and precipitation) during the breeding season. We show that hot and humid environments are associated with high species richness. In addition, our pilot results suggest that social systems are predicted by both dry and hot climate since nest building was associated with short breeding season in species rich environments. Moreover, nest building and clutch/tadpole attending appears to facilitate male territorial defence. In conclusion, environmental factors seem to influence breeding season length and reproductive modes, and these adaptations gave rise to various social behaviours, like territoriality.

Prolactin concentrations predict parental investment and nest survival in a free-living shorebird

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Hormone milieu during reproduction is one of the key factors that can influence the trade-off between reproductive investment and self-maintenance. Much of previous work has focused on prolactin as a physiological mediator since prolactin is involved in the onset and maintenance of parental care. However, how the prolactin relates to reproductive success in terms of altering parental behavior in wild populations is rarely investigated. Here we report the prolactin concentrations in breeding Kentish plovers (*Charadrius alexandrinus*) – a small shorebird that exhibits variable mating system and parental care, and thus used as an ecological model system of mating system evolution. Throughout the breeding season, we estimated the circulating prolactin concentrations of male and female plovers during incubation. In addition, we monitored the behavior of parents and determined the fate of their nest. We found that prolactin increased with clutch completion date, and incubating males and females with high prolactin concentrations invest more in incubation than those with low prolactin concentrations. Importantly, higher prolactin concentrations in either male or female predict higher nest survival. Our results suggest that prolactin is an indicator of parental behavior in a wild shorebird population, although experimental manipulations of prolactin are necessary to verify this relationship.

Comparative study of nest incubating sharing in three breeding Malagasy plover

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Based on the results of transponder tag data, the three studied species showed different rates of incubating sharing between day and night and times of day, and their contribution may vary according to the nest's ages.

Parental care patterns are associated with the mating opportunities in Chinese penduline tits *Remiz consobrinus*

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Parental care is one of the most diverse social behaviours, since the type and duration of care and the sex of the care provider may vary both within and between species. Theoretically, by caring or deserting the parents are expected to trade-off the benefits of offspring provisioning and thereby increase their survival against the costs such as lost mating opportunities. Due to different costs and benefits of caring, the interests of males and females over caring may also differ. Although theoretical studies have emphasized the significance of mating opportunities influencing parental decisions, the empirical evidence from wild populations is scanty. Here we investigate Chinese penduline tit *Remiz consobrinus*, a small passerine bird that exhibits four types of parenting within a single population: biparental care, female-only care, male-only care and biparental desertion. We show that seasonal variation in male and female care strategies are related to sex-differences in mating opportunities since early clutches are deserted by males and cared for by females, whereas late clutches are cared for by males and deserted by females. We show that the shift from deserting to caring is associated with seasonal variation in mating time of males, because late-breeding males take significantly longer to find a mate than early-breeding males. Taken together, our study supports theoretical studies showing that mating opportunities have implications for parental decisions. Future studies should experimentally manipulate mating opportunities to evaluate the effects of mating opportunities on parenting decisions in wild populations.