Biased sex ratios: evolutionary significance and consequences for conservation biology

Final report for grant no. KH 130430
Reporting period: 01.12.2018 - 30.11.2021

1. Background

The aim of the project was to investigate the role of a key demographic variable, the adult sex ratio (ASR), in the evolution of reproductive behaviour in animals. In an earlier publication (Liker et al. 2013, Nature Communications 4: 1587) we showed that ASR is strongly associated with both the mating system and parental care in shorebirds (Aves, suborder Charadrii), a clade that has a particularly high interspecific diversity in reproductive behaviour. That study was based on a small number of species, thus to test the robustness of its conclusions we generated and analysed a substantially extended dataset in the current research. The other main aim of the project was to provide new ASR data in shorebirds, using a novel statistical approach. To achieve this goal, we initiated a new field project to investigate the demographic characteristics and reproductive behaviour of the polyandrous pheasant-tailed jacana (*Hydrophasianus chirurgus*). Although we originally planned to investigate the demography of several shorebird species, this was not feasible both due to travel restrictions associated with the Covid-19 pandemic in 2020-2021, and also because working at multiple sites would need more capacities (both human and financial) than those we have had for the project. To decrease the impact of the pandemic-related delays, the project's duration was extended by one year, thus we were able to successfully implement fieldwork in two years (2019, 2021). In this final report, we provide brief summaries of our published studies, and describe the unpublished results in more details. Besides the work we planned in the proposal, we completed several other studies closely related to the objectives of the grant, which we also summarise in this report.

2. Studies within the main objectives of the grant

<u>2.1. Testing the relationship between ASR and sex roles in shorebirds (objective 1. in the grant proposal):</u>

The main question of this study was whether the evolution of mating and parental behaviour in shorebirds can be related to interspecific differences in adult sex ratios. We addressed this question using the comparative approach, i.e. by collecting data on both reproductive behaviour and ASR of different shorebird species, then analysing the associations by phylogenetically controlled statistical methods. In addition to testing the possible role of ASR, we extended the study by testing additional ecological hypotheses that propose other social and environmental factors that may influence sex role evolution in shorebirds (i.e. breeding density, nest predation rate, habitat productivity).

According to the work plan of the proposal, we increased the ASR sample size from the original 18 (Liker et al 2013) to 41 shorebird species, the full dataset containing 157 ASR estimates from >80 populations. We also collected information on the breeding density, hatching success (as a proxy for nest predation rate), Normalized Difference Vegetation Index (NDVI, as a proxy for food availability), as well as mating system (frequency of polygamy) and parental care for all of these 41 species. The associations of the social and ecological predictors with interspecific variation in sex role components were tested using phylogenetic generalized least squares (PGLS) models. Our results show that both mating system and parental care are strongly and significantly associated with ASR of the species (Fig. 1), replicating the results obtained in our earlier study (Liker et al. 2013). This goes in line with the mating opportunity hypothesis stressing the importance of the proportions of sexes in the populations: a male-biased ASRs provides higher mating opportunity for the females and a low opportunity of mating for the males, thus is associated with female polyandry and predominant male care, whereas female-biased ASRs are associated with male polygyny and female care.

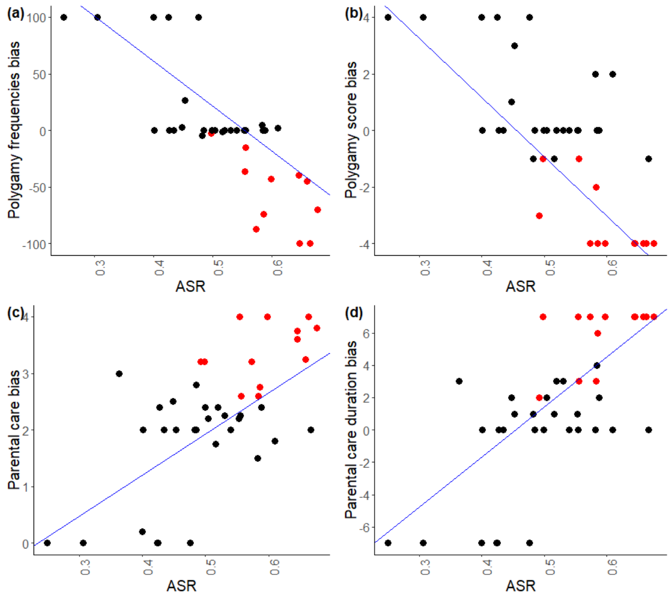

Fig. 1. Relationship between adult sex ratio (ASR, number of adult males/number of adult males plus adult females in the population) and components of sex roles in shorebirds. ASR is negatively associated with (a) polygamy frequency bias (% male polygamy – % female polygamy), (b) polygamy score bias (male polygamy score – female polygamy score), and positively associated with (c) parental care bias (average score for relative male participation in 5 parental care activities: nest building, incubation, nest guarding, chick brooding, chick guarding), and (d) parental care duration bias (male care duration – female care duration). Black and red dots represent conventional and sex-role reversed species, respectively (n= 36, 39, 41, 41 species). Regression lines indicate significant relationships and were estimated by the PGLS models.

Besides, our results show that the breeding density of a species is also strongly associated with parental care as we found that the frequency of male polygamy decreases whereas the amount of parental care by males increases with breeding density (Fig. 2). Interestingly, there is an interaction between the effects of ASR and breeding density on sex roles: the effect of adult sex ratio on polygamy frequency bias is stronger in high breeding density compared to populations with low breeding density (Fig. 3). This latter result is in line with theoretical expectations and some empirical studies suggesting that the rare sex has especially good mating opportunities in high density populations. Finally, we also found a significant negative association between parental care and NDVI, suggesting that males tend to provide less care during incubation and chick rearing when the habitat is more productive (e.g. where food availability mag be higher), although this relationship is much weaker than the effects of ASR or breeding density.

In sum, the study corroborates the conclusion of our earlier paper that ASR is a good predictor of sex roles in shorebirds, and suggest that polygamy and highly sex-biased parental care can be expected in species that are characterised by biased adult sex ratios and high breeding densities. This study also shows that other ecological factors, like the productivity of the breeding habitats and nest predation rates, may have less influence on sex role evolution in shorebirds than previously thought. These results were presented at two conferences (***Fresneau et al. 2021a,b***). We are in the process of writing a manuscript that we expect to submit to a peer reviewed international interdisciplinary/evolutionary journal in 2022 (***Fresneau et al., Manuscript 1***).

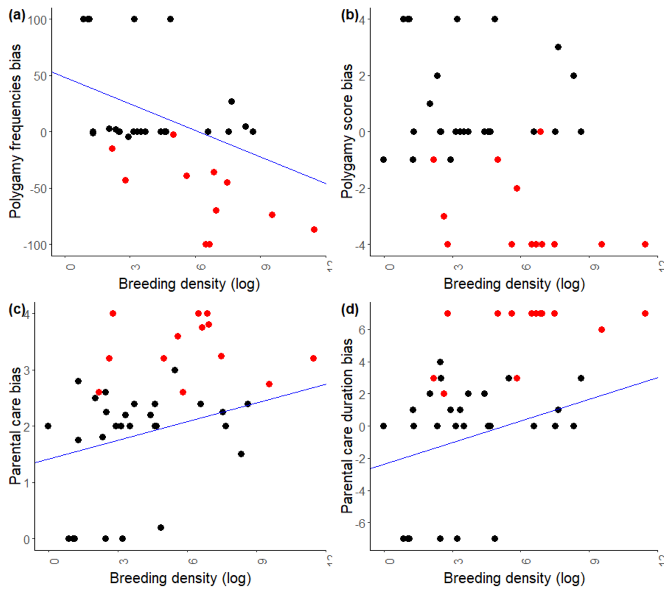

Fig. 2. Relationship between breeding density and components of sex roles in shorebirds. Breeding density (pairs per km^2) is negatively associated with polygamy frequenciy bias (a), and positively associated with parental care bias and parental care duration bias (c-d). See Fig. 1. for explanations of symbols and for sample sizes.

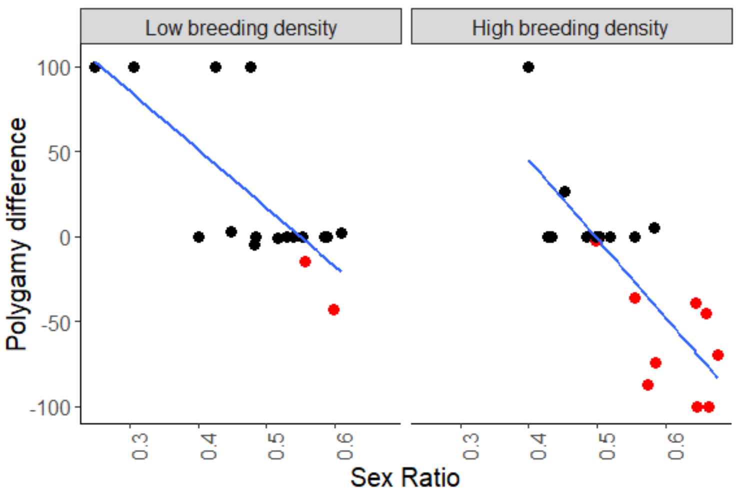

Fig. 3. Relationship between ASR and polygamy frequency bias in species characterised by low breeding density (left) and high breeding density (right). ASR and breeding density has a statistically significant interaction effect on polygamy frequency bias, with a steeper negative relationship in species that breed at higher population densities. See Fig. 1. for further explanations, n= 36 species.

2.2. Field studies of ASR and reproductive sex roles in shorebirds (objective 2. in the grant proposal):

The aims of this part of the project were to conduct fieldwork (1) to provide new ASR estimates for shorebird species in which the sexes have distinct reproductive sex roles (e.g. sex-role reversal), (2) to explore which demographic processes generate unbalanced ASRs, and (3) to produce new data on their reproductive behaviour. In 2019, we started a new field study to investigate these questions in wild pheasant-tailed jacana populations. This Asian jacana species is a textbook example of classical polyandry and sex-role reversal, but only a few studies have investigated its reproductive biology and the demographic properties of their populations are completely unknown. Thus, it represent an excellent model system for investigating the drivers of sex role evolution, including the effects of the biased adult sex ratio.

The study has been conducted in two locations. In the first year (2019), we conducted 3 months of fieldwork in the Pheasant-tailed Jacana Educational Park in Guantian (Tainan, Taiwan) from June to September. In 2020, we were not able to organize fieldwork due Covid-19-related travel restrictions. In May-August 2021, we managed to continue the study in a wetland area near Khon Kaen, Thailand (in collaboration with Dr. Wangworn Sankamethawee, University of Khon Kaen). We needed to change the study site because in Taiwan it was not feasible to gather necessary data for demographic studies, whereas these are possible in the new Thai collaboration. We successfully obtained all authorizations from the Thai government that are necessary for conducting long-term research in the country. In 2019 and 2021, we developed the methodologies for studying the breeding biology and demography of the jacana populations. Pheasant-tailed jacanas breed on floating vegetation in tropical wetlands, which make the fieldwork challenging. For example, to measure population demographic parameters (sex ratio at hatching, survival rates, age of sexual maturation etc.), it is necessary to catch and individually mark both the adult birds and their offspring and to follow the fate of the individuals through a long period (several years). To make this possible, we had to develop numerous new technics including using a decoy with sounds for attracting territorial individuals into the nets (Fig. 4) and trapping adult birds on the nest using a floating trap (Fig. 5)***.***

Fig. 4. Setup for catching adult pheasant-tailed jacana using a net (in the background) and a decoy (in the front) and recorded sounds.

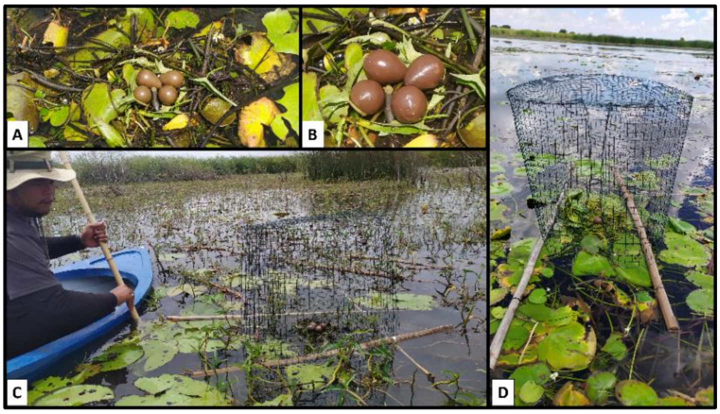

Fig. 5. Setup for catching breeding adult male pheasant-tailed jacanas on the nest using a floating trap. The eggs (A) are replaced with dummy eggs (B) in order to protect real eggs for being broken during catching. Then we place the floating trap on the nest.

(1) Estimating the adult sex ratio of the populations: One of the main current hypotheses on the evolution of sex-role reversal is based on sex differences in mate availability, e.g. that male-biased ASRs promote the development of female competition for mates and male parental care (see section 2.1. above). Sex ratio is thus a key variable in studying the evolution of mating system, but in most studies its estimation is either based on simple population census (which can be highly inaccurate) or on long-term population monitoring using a large number of marked individuals (which needs much effort and time). During our fieldwork in Taiwan and Thailand, we used extensive but time-effective weekly population censuses to count adult males and females repeatedly over the breeding seasons (see Fig. 6. for an example of the census site in Thailand). Then we applied a new statistical approach developed for census data of unmarked individuals (N-mixture modelling), that allows (1) to estimate accurately the number of individuals in each sex (hence ASR) using the repeated counts, (2) to take in account individuals that we could not sex in the censuses, and (3) to estimate potential sex-specific detectability biases. We completed the statistical analyses of the data collected in Taiwan, and are currently finishing the data analyses for the Thailand population. In line with the prediction of the mate availability hypothesis, preliminary results suggest a consistently male-biased ASR in both jacana populations (the proportion of males being between 0.6 - 0.7; Fig. 7-8). The N-mixture model corroborates an overall male-bias in the Taiwan population, and the weekly estimates suggest a seasonal change in the ASR (Fig. 7). A similar seasonal trend may also be present in the ASR of the Thailand population (Fig. 8), although we still need to finish the statistical analyses to support this. These results are important because these represent one of the few good quality ASR estimates available for any sex-role reversed species, and no comparable data exist for any jacana species despite that these are the most iconic examples for sex-role reversal. The study also demonstrates the usefulness of the N-mixture modelling statistical approach, thus will likely promote the use this method that can lead to better quality field estimates for ASR in other species. We have presented these results in conference talks (***Fresneau et al. 2020, 2022a,b***). We prepared a manuscript reporting the Taiwan study that we are currently updating with the results from Thailand and plan to submit in 2022 (***Fresneau et al., Manuscript 2***)

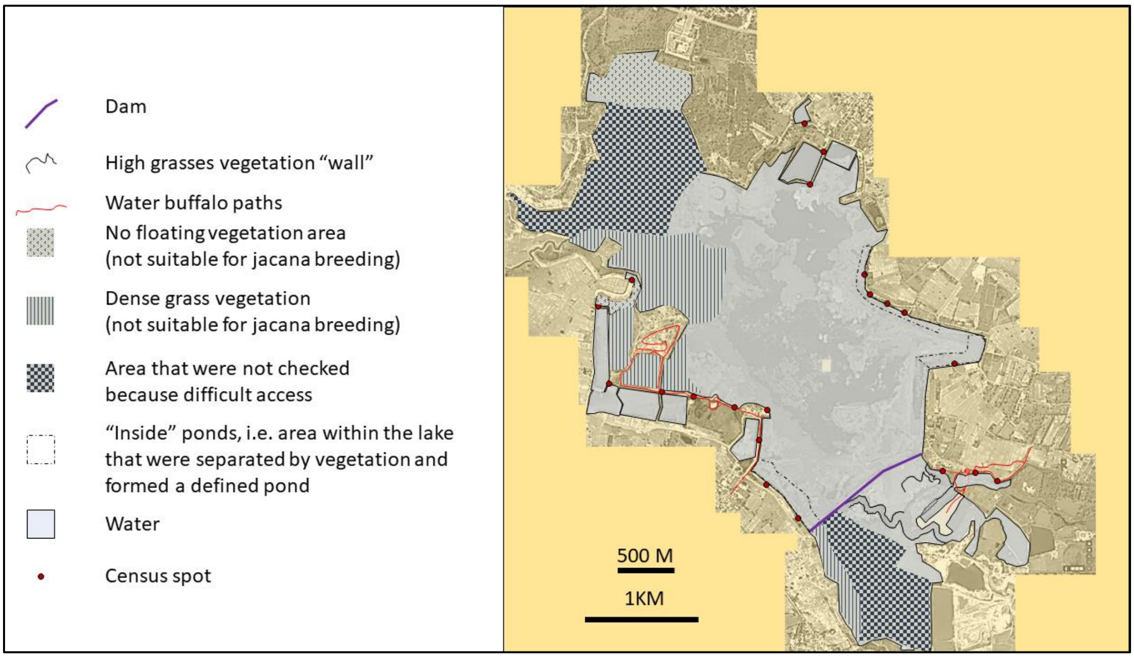

Fig. 6. Map of the field site in Thailand, Lake Kaeng Nam Ton, showing the different type of vegetation and the census plots we used for weekly ASR estimation.

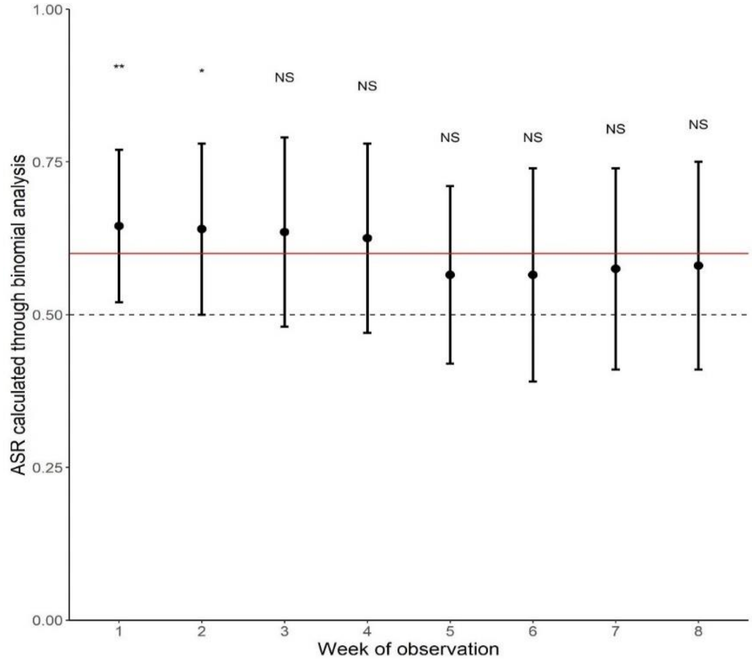

Fig. 7. ASR estimates for the pheasant-tailed jacana population in Taiwan between June and August 2019. Data points represent the observed ASR, error bar represent the 95% CI obtained from the binomial test for each week, and significance of the weekly observations indicates statistical difference from a balanced sex ratio (i.e. ASR = 0.5; ** P <0.01, * P <0.05, NS nonsignificant). The red line represents the overall ASR estimate obtained from the N-mixture model analysis of the repeated (weekly) censuses.

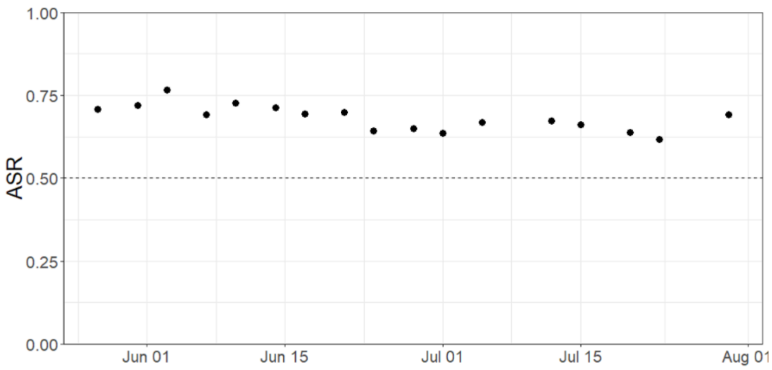

Fig. 8. ASR estimates for the pheasant-tailed jacana population in Thailand between May and August 2021. Data points represent the ASRs observed in weekly censuses (mean ± SE: 0.68 ± 0.01, n= 17 censuses).

<u>(2) Drivers of the sex ratio bias:</u> In this part of the project, we aimed to identify those demographic processes that can result in the highly male-biased ASR of the jacana populations. These processes include a male-biased birth sex ratio, a longer time to reach sexual maturity for female than male jacanas, and a higher mortality rate of females in at least some part of the life cycle (e.g. during development, or as adults, or both). Testing the role of these processes requires a study at least a few years long, because jacanas breed seasonally and data from several years are needed to provide good estimates for demographic variables. Since we were not able to work in 2020 due to the Covid-19 pandemic, and needed to change the study site from Taiwan to Thailand, we were only able to initiate these demographic studies (and lost the effort we invested in Taiwan). Nevertheless, we ringed both young and adult birds in both populations and collected samples from hatchlings for genetic analyses

to estimate the offspring sex ratio. We completed the sexing of the hatchlings from the Taiwan samples, and corroborated the accuracy of the method using samples of adults with known sex. Sexing of the Thailand samples are in progress (conducted in the lab of our Thai collaborators because the samples cannot be exported from the country). We are planning to continue the data collection for all demographic variables in Thailand in the next few years, for that Dr Nolween Fresneau won an NKFIH postdoctoral research grant (PD 134414, duration: 2020-2023).

(3) Sex roles in the pheasant-tailed jacana: We conducted detailed observations to study the reproductive behaviour of males and females, because this has been poorly described in this highly data-deficient species. We found that females provide most of the territory defence toward conspecifics. Males also participate in agonistic behaviours, although less frequently than females. Furthermore, contrary to what is expected for a sex-role reversed species, we found that males spent more time than females on courtship behaviour. Polyandrous females performed mating and laying sequentially with several different mates, but maintained the pair bonds simultaneously with multiple males. For the first time for the species, we could estimate that the average number of mates per female (i.e. degree of polyandry) was 2.4 and that at least 82 % of the females in the population were polyandrous. Finally, our observations corroborated that brood care is predominantly provided by males, although females were also participating to some degree in brood attendance but never in direct care (i.e. brooding). This study highlights that some aspects of polyandrous breeding might deviate from stereotyped view on sex-role reversal and stress the importance of further within-species and comparative studies to fully understand the mechanisms leading to sex-role reversal. We presented these results at three conferences (***Fresneau et al. 2019a,b, Liker & Fresneau 2019***), and published in a paper (***Fresneau et al. 2021, Frontiers in Ecology and Evolution***).

Linked to our research on pheasant-tailed jacanas, we continue to strengthen our collaborations with leading international researchers investigating the ecology, sex roles and conservation of shorebirds (Élvonal Shorebird Science network, University of Debrecen, principal collaborators: Prof Tamás Székely & Dr Vojtěch Kubelka). They organize and conduct similar studies on several species worldwide (for further information see: https://elvonalshorebirds.com), and we collaborate with their projects to build up multispecies dataset that can form the bases for further comparative studies. Furthermore, we advertise the project in Thailand and involve local students and assistants in our fieldwork. The project was presented to the wider audience in an online seminar at the Khon Kaen University (***Fresneau 2021***).

2.3. The relationship between adult sex ratio and population viability (objective 3. in the grant proposal):

In this part of the project we tested the prediction of theoretical models that ASR of the populations can influence their productivity, and hence even can affect their long-term viability (see the underlying models in the research proposal). We attempted to investigate this problem using the same dataset of population ASRs of shorebirds we described in section 2.1 (above). As a proxy for population viability, we used recently published world population trends for shorebirds (BirdLife International: IUCN Red List for birds, http://www.birdlife.org/datazone/species, published in 2020), that were available for 32 of the 41 species with available ASR estimates. We analysed the association between population trends and ASR using phylogenetic generalized linear models. The results suggest that the population trends of shorebirds (i.e. decreasing versus increasing/stable) is not related to variation in ASR (***Fig 9.***). This result is robust to the potential confounding effect of mating system because the statistical model that include mating system produce the same conclusion (both the ASR and the interaction effects are non-significant). Although these preliminary results do not support the predicted effects of ASR on population viability, the analyses may lack power due to the small sample size, and also because the proxy we used for population trends has only a very rough resolution. We are planning to develop further this study by obtaining more accurate data on the productivity of shorebirds, e.g. by collecting data on reproductive success for those populations for that we also have ASR estimates. We produced a brief review of theories and published evidence on how ASR can influence productivity and population viability, and is going to publish this in a paper that will be submit in early 2022 (***Schacht et al., Manuscript 3***).

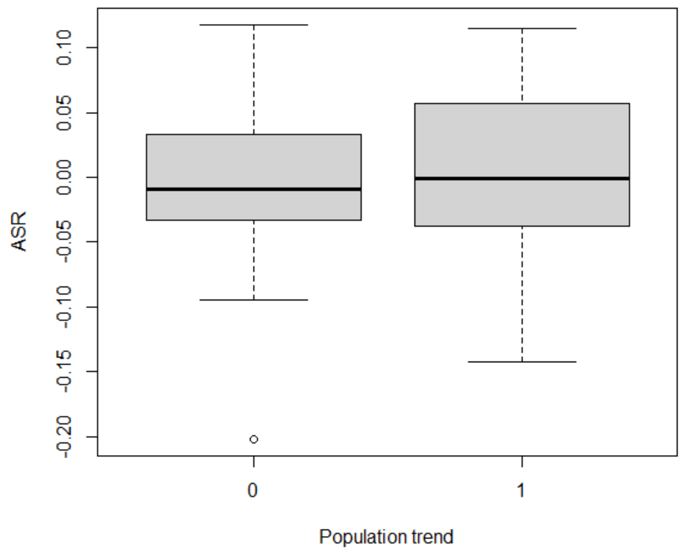

Fig. 9. ASR is not related to the population trends of shorebirds (ASR is shown on a normalized scale; for population trends 0: declining, 1: stable or increasing, according to the assessment by the BirdLife International 2020 IUCN Red List for birds; n= 32 species).

3. Studies closely related to project:

During the reporting period, we completed several other studies that focused on topics closely related to the main questions of the project. Below we briefly summarise the results:

<u>3.1. Demographic drivers of the interspecific variation of ASR:</u>

In a follow-up project to our earlier study (Pipoly et al. 2015, Nature), we investigated which demographic processes can link the type of sex determination (XY or ZW) to ASR variation in tetrapods (450 species of reptiles, birds, mammals). We show that XY and ZW species differ in sex-specific adult mortalities. Variation in ASR is predicted by sex-specific juvenile and adult mortalities, and also by sex differences in age of maturation. Thus these results suggest that the type of sex determination is linked to ASR through an effect on sex-specific adult mortality. We presented the results at four conferences (***Liker et al. 2019, Pipoly et al. 2020a,b, and 2021***) and in a manuscript we are preparing for publication (***Pipoly et al., Manuscript 4***).

Using data for 200 bird species, we showed that male-biased ASR is associated with delayed female maturation, whereas female-biased ASR is associated with delayed maturation in males. Phylogenetic path analyses suggest that biased ASRs drive changes in the intensity of sexual selection which, in turn, results in delayed maturation in the sex experiencing more intense sexual selection (***Ancona et al. 2020, Evolution Letters***).

We collaborated in a comparative project which, using the largest available dataset to date, investigated sex differences in lifespan in 101 mammal species. We showed that, similarly to humans, female mammals generally have longer lifespan than males (***Lemaître et al. 2020, PNAS***).

We tested whether sex differences in adult mortalities in birds is related to sex differences in parasite infections. We show that parasite prevalence is not different between adult males and females. We found no correlation between sex-biased host mortalities and sex-biased parasite prevalence. These results were consistent in both blood and gastrointestinal parasites (***Valdebenito et al. 2020, Scientific Reports***).

3.2 Comparative studies of the associations between ASR and reproductive sex roles:
We showed that, in opposition to the common assumption, males are typically larger than females in tetrapod species that are characterised by female-biased ASR. The scarcity of the larger sex is not explained by its higher mortality, because sex differences in mortality does not predict sexual size dimorphism (SSD). Instead, phylogenetic path analyses suggest that sex-biased mortality leads to skewed ASR, which in turn has a knock-on effect on SSD due to more intense sexual competition in the rare sex (***Liker et al. 2021, Evolution***).

In a comparative study of 81 reptiles, we found that the frequency of multiple paternity of clutches increases with male-bias in adult-sex ratio, supporting that either female choice or forced copulations by males can lead to genetic polyandry when there are more males than females. Our study also shows that multiple paternity differs consistently between sex-determination systems in reptiles: species with ZW sex determination have the highest frequency of multiple paternity, while and species with XY sex determination have the lowest frequency of multiple paternity. We presented the results in a talk (***Mészáros et al. 2019***) and submitted a manuscript for publication (***Pipoly et al., Manuscript 5***).

In the most detailed analyses of avian sex roles to date, we investigated which ecological, life history and social factors predict sex roles. We found that climate and life-history show weak associations with sex roles. However, adult sex ratio is associated with sexual dimorphism in size and ornamentation, mating system, and parental care, suggesting that social environment is central to explaining variation in sex roles among birds (***Gonzalez-Voyer et al. 2022, Ecology Letters***).

We showed in frogs that in cool and humid climates males provide offspring attendance, whereas in more predictable temperatures endotrophy occurs, whereby the female provides all nutrients for the offspring until metamorphosis. In addition, we found that uniparental clutch attendance by males is present in species with territorial defence, whereas cooperative nest building co-occurs with sperm competition. The type of parental care is not associated with adult sex ratios (***Vagi et al. 2020, Global Ecology and Biogeography***).

3.3 Comparative studies of the evolution of reproductive traits:
We collaborated in a comparative study that tested large-scale phylogenetic patterns in the duration of developmental time for 3096 avian species. Developmental phases associated primarily with growth are the longest and most variable, consistent with a role for allometric constraint in determining the duration of development. Developmental durations retain a strong imprint of deep evolutionary history, while body size differences among species explain less variation than previously thought. Developmental duration is associated with ecological variables, including the relative safety of nest and pressures of breeding phenology (***Cooney et al. 2020, Nature Communications***).

Consistently with the classical hypothesis of Jarman (1974), phylogenetically controlled analyses of ungulates confirmed that ecology predict group size, since grazing ungulates typically live in open habitats and form large herds. Group size, in turn, has a knock-on effect on mating systems and sexual size dimorphism, since ungulates that live in large herds exhibit polygamy and extensive sexual size dimorphism. Phylogenetic confirmatory path analyses suggest that evolutionary changes in habitat type, feeding style and body size directly (or indirectly) induce shifts in social organization (***Szemán et al. 2021, Journal of Evolutionary Biology***).

Finally, we used comparative data to test a basic assumption of current sexual selection theories, the Darwin–Bateman paradigm. This hypothesis argues that the root of the evolution of the diversity of sex roles in animals is anisogamy (i.e., differences in size and/or function of gametes between the sexes) that leads to biased sexual selection, and sex differences in parental care and body size. Our results question the first step of the Darwin–Bateman paradigm, as the extent of anisogamy does not appear to predict the intensity of sexual selection. The only significant predictor of sexual selection is the relative inputs of males and females into the care of offspring (***Mokos et al. 2021, Scientific Reports***).

4. References:

4.1. Published papers:

Ancona S, Liker A, Carmona-Isunza MC & Székely T 2020. Sex differences in age-to-maturation relate to sexual selection and adult sex ratios in birds. ***Evolution Letters***, 4: 44-53.

Cooney, C. R., Sheard, C., Clark, A. D., Healy, S. D., Laland, K. N., Liker, A., Street, S.E., Troisi, C., Thomas, G.H., Székely, T., Hemmings N. & Wright, A.E. 2020. Ecology, phylogeny, and the evolution of developmental duration in birds. ***Nature Communications***, 11: 2383.

Fresneau, N., Lee, Y.-F., Lee, W.-C., 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.

Gonzalez-Voyer A, Thomas GH, Liker A, Krügger O, Komdeur J, Székely T 2021. Sex-roles in birds: phylogenetic analyses of ecology, life histories and social environment. ***Ecology Letters*** (in press)

Lemaître, J., Ronget, V., Tidière, M., Allainé, D., Berger, V., Cohas, A., Colchero, F., Conde, D., Liker, A., Marais, G., Scheuerlein, A., Székely, T., Gaillard, J. 2020. Sex differences in adult lifespan and aging rates of mortality across wild mammals. ***Proceedings of the National Academy of Sciences USA,*** 117: 8546-8553.

Liker A, Bókony V, Pipoly I, Lemaitre JF, Gaillard JM, Székely T & Freckleton RP 2021. The evolution of large males is associated with female-skewed adult sex ratios in tetrapods. ***Evolution***, 75: 1636-1649

Mokos J, Scheuring I, Liker A, Freckleton RP, Székely T 2021. Anisogamy does not predict the origin of sex roles, ***Scientific Reports***, 11: 19424.

Szemán K, Liker A, Székely T. 2021. Social organization in ungulates: revisiting Jarman's hypotheses, ***Journal of Evolutionary Biology***, 34: 604-613.

Valdebenito JO, Halamibieke N, Figuerola J, Liker A, Székely T. 2020. Mortality cost of sex-specific parasitism in wild bird populations, ***Scientific Reports***, 10: 20983.

Vági B, Végvári Z, Liker A, Freckleton RP, Székely T 2020. Parental care forms are predicted by climatic and social environments in Anura. ***Global Ecology and Biogeography*** 29: 1373-1386.

4.2. Manuscripts:

Fresneau N, Pipoly I, Gigler D, Kosztolányi A, Székely T, Liker A The evolution of reproductive sex roles in shorebirds: a test of three hypotheses of sex-role reversal (Manuscript 1, in preparation).

Fresneau N, Sankamethawee W., Lee Y-F, Lee W-C, Kosztolányi A, Székely T, Liker A. Measuring adult sex ratio in the wild: an application of new techniques using the pheasant-tailed jacana (*Hydrophasianus chirurgus*) (Manuscript 2, in preparation).

Pipoly I, Bókony V, Gaillard J-M, Lemaitre J-F, Székely T, Liker A Demographic pathways linking interspecific variation in adult sex ratio to genetic sex determination systems in tetrapods (Manuscript 4, in preparation).

Pipoly I, Duffy R, Mészáros G, Bókony V, Vági B, Székely T, Liker A Multiple paternity is related to adult sex ratio and sex determination system in reptiles (Manuscript 5, submitted, Journal of Evolutionary Biology).

Schacht R, Beissinger SR, Wedekind C, Jennions M, Geffroy B, Liker A, Kappeler P, Weissing F, Kramer K, Hesketh T, Boissier J, Uggla C, Holingshaus M, Székely T Adult sex ratios: causes of variation and implications for animal and human societies (Manuscript 3, in preparation)

4.3. Conference presentations:

Fresneau N, Lee YF, Lee WC, Liker A 2019a. How to deal with love triangles in the Pheasant-tailed Jacana Hydrophasianus chirurgus? Talk. International Wader Study Group annual conference, 19-23 September 2019, Morecambe Bay, UK.

Fresneau N, Lee YF, Lee WC, Liker A 2019b. Pair-bonding and parental behaviour of the sex-role reversed pheasant-tailed jacana. Talk. Magyar Etológiai Társaság XXI. Konferenciája, 2019. november 29. – december 1., Mátrafüred.

Fresneau N, Lee Y-F, Lee W-C, Kosztolányi A, Székely T, Liker A. 2020**.** The Pheasant-tailed Jacana, its sex-ratio, and pair bonding: story of a sex reversed and polyandrous bird. Talk. III. ÉLVONAL Conference, 10–12 January 2020, Debrecen, Hungary.

Fresneau N 2021. The peculiar breeding of the Pheasant-tailed jacana: study of a population in Kaeng Nam Ton. Invited talk, Department of Environmental Science, University of Khon Kaen, September 2021 (online).

Fresneau N, Pipoly I, Gigler D, Kosztolányi A, Székely T, Liker A. 2021a. The evolution of sex-roles in shorebirds: a test of three hypotheses. Talk. IV. ÉLVONAL Conference: Sex roles and breeding ecology of shorebirds. 8-9 January 2021, Debrecen (online).

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