Final report

"Group functioning and patterns of social interactions" K112527 by Zoltán Barta

1. Introduction

Individual differences in behaviour, which are consistent over time and contexts, are defined as animal personality. In social species, individual-level behaviour, hence personality, is expected to directly influence group-level behaviour, and therefore to shape several aspects of sociality. The aim of the project was to link individual- and group-level behaviours by studying the relationship between individual personality and forms of social behaviour, and the effect of personality on group functioning. More specifically, we investigated the relationships between personality and social dominance, personality and social foraging tactic use (producerscrounger game), and social and spatial patterns of flocking under natural conditions. Furthermore, we studied the effect of groups' personality composition on the state of individuals and the groups' innovative problem solving capacity in a novel foraging task experiment.

We investigated the proposed topics in two closely-related passerine species, the Eurasian tree sparrow (*Passer montanus*) and the house sparrow (*Passer domesticus*). The two species were selected as model organisms since they are highly gregarious under natural conditions and exhibit diverse forms of social behaviour (i.e. social dominance, social foraging, etc.) that were targeted by our studies. Within the frame of the project all the work on free-living individuals was carried out on tree sparrows, while experimental studies were performed on house sparrows.

Tree sparrows were investigated at the Central Campus and Botanical Garden of the University of Debrecen (Debrecen, Hungary). The study site is mainly an open area with scattered trees and bushes, also containing some buildings of various sizes forming a heterogeneous semi-urban landscape mosaic. Tree sparrows regularly breed in small numbers at our study site and winter there in large flocks. During winter birds forage predominantly on our bird feeders. Tree sparrows are apparently monomorphic, individuals cannot be sexed based on plumage or morphological characteristics alone. Both sexes possess a black bib patch, which is a melanin-based plumage signal with a partly known signalling function.

Experimental work on house sparrows was carried out at indoor aviaries located at the Zoology Campus of Babes-Bolyai University (Cluj Napoca, Romania) in collaboration with the Evolutionary Ecology Research Group from the Hungarian Department of Biology and Ecology, Babes-Bolyai University. House sparrows have a similar ecology and life-history to tree sparrows. Furthermore, house sparrows are also highly social and exhibit the same range of social behaviours as tree sparrows. In contrast with tree sparrows, house sparrows are sexually dimorphic and are slightly larger in size.

2. Results

Within the frame of the project we have completed several studies under both natural and laboratory conditions, using both correlative and experimental approaches. Some of the studies were already published, while others are under consideration or in preparation to be published.

2.1. Status signalling in male but not in female Eurasian Tree Sparrows *Passer montanus* (Mónus et al. 2016, IBIS)

Male ornaments, such as plumage coloration, frequently serve as signals. The signalling function of similar ornaments in females has, however, received much less attention despite the fact that conspicuousness of their ornaments is often comparable to those of males. In this study we tested the signalling function of a plumage trait present in both sexes in the Eurasian Tree Sparrow Passer montanus. The black throat patch has been repeatedly found to have a signal function in the closely related House Sparrow Passer domesticus, where only males bear the ornamental trait. However, the function of the black throat patch in the females of Passer species that have sexually monomorphic ornament expression has never, to our knowledge, been considered. We investigated the outcomes of aggressive encounters in foraging flocks of free-living Tree Sparrows, and assessed whether throat patch size and measurements of body size predicted fighting success in these flocks. We found that male throat patch size predicted fighting success against both male and female opponents. However, female throat patch size did not correlate with fighting success against either sex. Among the morphological traits studied, wing length was the best predictor of fighting success in females. Our findings suggest a status signalling function of throat patch size in males but not in females, although further experimental studies are necessary to corroborate these correlative results.

2.2. The relationship between social foraging tactic use and individual personality (Fülöp et al. 2019, BEHAV ECOL)

Social foraging is an important aspect of group living, determining individual fitness. In this study, we have investigated the relationship between individual personality and social foraging tactic use (i.e. producing or scrounging) in free-living tree sparrows during three wintering seasons (between 2013-2016). During all three seasons we have captured, marked and tested for personality 189 individuals (78 males and 111 females), than, during the last two winters of the study (between 2014-2016), we have recorded social foraging behaviour of individuals on multiple feeders at our study site. First, using data from individuals that were tested multiple times, we have confirmed that exploratory behaviour, measured using the standard open-field test, is a repeatable behavioural trait in tree sparrows, and thus, it is an axis of individual personality in this species. Then, we have investigated the relationship between exploratory behaviour and use of social foraging tactics, and found that exploratory behaviour was sexdependently related to the proportion of scrounging: while in males exploratory behaviour was not related to foraging tactic use, in females exploratory behaviour and the probability of scrounging were positively related. Additionally, we found that probability of scrounging was positively influenced by the density of foraging individuals, and the time of feeding within the foraging bout, that is, the later the individual foraged within a foraging bout the higher the probability of scrounging was. Our results indicate that consistent individual behavioural differences are linked, in a sex-dependent manner, to group-level processes in the context of social foraging in free-living tree sparrows.

2.3. The relationship between social dominance and individual personality (Fülöp et al. 2020, in preparation, proposed journal: ETHOLOGY)

In group-living animals social dominance status is a primary determinant of individual fitness. Dominance status of individuals can be influenced by a series of individual features (e.g. sex, body size, personality) and is also frequently signalled towards conspecifics through various conspicuous colourful traits. Individual personality is a behavioural attribute often associated with social dominance status, yet, based on earlier studies, the relationship between personality and dominance status is far from being straightforward. In this study, we have investigated the relationship between social dominance and individual personality in free-living tree sparrows during three wintering seasons (between 2013-2016). Specifically, we studied whether

exploratory behaviour predicts social dominance status in free-living tree sparrows during winter while taking into account sex and body size. Additionally, we investigated the dominance signalling role of the black bib patch (hereafter "bib") of individuals, a conspicuous melanin-based plumage ornament with a poorly known signalling value in this species. We found that dominance status of individuals, expressed by two measures, proportion of aggressive fights initiated and fighting success, was not predicted by exploratory behaviour, but was positively correlated with body size, independently of sex. Furthermore, bib size of individuals sex-dependently indicated their dominance status for one of the two measures: bib size was positively correlated with the proportion of fights initiated in females, but not in males. Our results suggest that, at least in this species, dominance status is determined primarily by physical traits of individuals (i.e. body size), rather than individual personality, or at least, not exploratory behaviour. Interestingly, our results hint that bib size might function as a dominance signal in females as well, a previously unknown function of the black bib in this sex.

2.4. Melanin signalling of individual personality and physiological state (Fülöp et al. 2020, BEHAV ECOL SOCIOBIOL, under revision)

Association preferences of individuals in groups may be influenced by the phenotype of potential group mates, which can be signalled towards conspecifics through plumage ornaments. Hence, we studied this by investigating the phenotypic correlates of the black bib, a melanin-based plumage ornament, possessed by both sexes in tree sparrows, during four winters (2016-2020). More specifically, we investigated the sex-dependent relationships between bib size and three aspects of individuals' phenotype: body condition (i.e. sizecorrected body mass), physiology (i.e. cellular innate immunity/inflammation status, expressed through total leucocyte counts, and chronic physiological stress, expressed through the ratio of heterophils to lymphocytes) and individual personality (i.e. activity in a novel environment). We found that bib size was not associated with body condition and cellular innate immunity/inflammation status, but was positively related to physiological stress levels independent of sex. Furthermore, bib size was negatively associated with activity in males but positively in females. Our results suggest that colourful plumage ornaments can have an important role in mediating social processes through signalling individual traits with confirmed social implications, and bring important correlative evidence that ornamental traits may have sex-specific signalling value even in species with no apparent sexual dimorphism.

2.5. Social organization of flocks across years (Fülöp et al. 2020, in preparation, proposed journal: AUK)

Social organization of flocks is one of the primary characteristics of groups which can have wide implications for individuals through various social processes (e.g. mate choice, predator avoidance, foraging efficiency). Social organization of flocks is primarily determined by the social and spatial preferences of individuals. Therefore, we studied the social organization of free-living tree sparrow flocks, covering both the social and spatial structure of flocks. We also studied how the interplay between previously established social relationships and space use shapes long-term social associations, and implicitly, the long-term consistency of social relationships. We collected data on the co-occurrence of previously marked individuals in flocks at multiple feeders from our study site during four winters (between 2015-2019). We characterized social structure of groups using social networks: we used association social networks to describe social aspects of flocking, while used bipartite social networks to characterize feeder use (i.e. space use) of individuals. We found that tree sparrows associated non-randomly and the structure of their social networks indicated multiple social communities (Fig 1.). Social structure of flocks, as measured by the structure of social networks, was jointly determined by individual social relationships and feeder use. Social communities tended to use different areas, which was indicated by the structure of both social network types. Over longterm (the four studied winters), the social structure of the flocks, as expressed by the association networks, were consistent, meaning that social relationships between familiar individuals were stable across years. Feeder use of individuals predicted their social associations, but interestingly, current social relationships were more strongly determined by individual relationships established during the previous year, and this pattern was found to be consistent over multiple winters. Long-term consistency of social relationships suggests that social stability between familiar individuals might be advantageous during the winter.

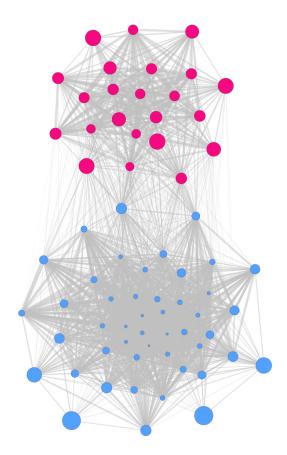


Fig 1. A sample weighted association social network of Eurasian tree sparrow (*Passer montanus*) individuals from the winter of 2017/18. Node sizes are proportional to the binary degree (i.e. number of associates) of individuals, while edge width to the association strength of individuals, expressed through the simple ratio index. Node colours mark different social communities determined based on the association network (pink: Botanical Garden, blue: Central Campus). Network visualization made in Gephi.

2.6. Home range and space use of tree sparrows (Fülöp et al. 2021, in preparation, proposed journal: IBIS)

In addition to the feeder use of individuals (see above study #2.4), which is an indicator of individual space use, we also investigated home rage size and space use of tree sparrows at our whole study site (Fig 2.). Six individuals (3 males and 3 females) were captured at two bird feeders at the end of January 2017 and were radio tracked for 2-4 weeks on a daily basis, depending on the activity period of the radio tags used. The two feeders where the individuals were captured were predominantly used by birds from different social communities (based on the results of the study #2.4). Beside the position of individuals recorded during daytime, roosting sites of all tracked birds were also recorded during the whole period of activity of the radio tags. We found that home ranges varied greatly both in size and shape (Fig 2.). In general, home ranges of birds captured at different feeders (i.e. in different social communities)

were spatially separated, but some showed a moderate overlap. Tracked birds used individual roosting sites and showed a high fidelity to their roosting places.

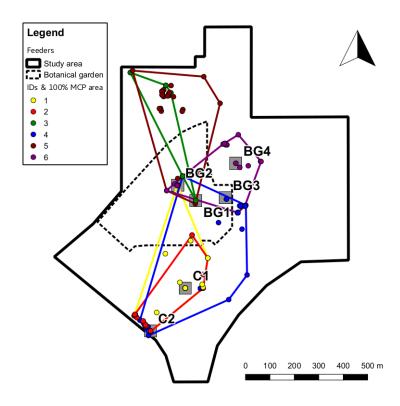


Fig 2. Schematic illustration of the study area covering the Central Campus (solid black line) of the University of Debrecen and the Botanical Garden (dashed black line) and the location of the feeders (BG1-4, C1-2). Home ranges of six radio-tagged Eurasian tree sparrows (*Passer montanus*), expressed through 100% minimum convex polygons (MCPs; indicated by the coloured polygons on the figure), are also show. MCPs were calculated using fixes (coloured points) collected during radio tracking. Colours mark different individuals; note that points on the map (e.g. at feeders) may overlap.

2.7. The effect of groups' personality composition on the physiological state of individuals (Vágási and Fülöp et al. 2020, PROC ROY SOC B, under revision)

Social groups often consist of diverse phenotypes, including different personality types, and this diversity is known to affect the functioning of the group as a whole. Social selection theory proposes that group composition (i.e. social environment) also influences the performance of individual group members. However, the effect of group behavioural composition on group members remains largely unexplored, and it is still contentious whether individuals benefit more in a social environment with homogeneous or diverse behavioural composition. We experimentally formed groups of house sparrows (*Passer domesticus*) with different

personality (i.e. exploratory behaviour) composition in terms of mean and variance of personality [random, high exploratory, low exploratory and variable (50% high + 50% low exploratory)] and measured changes in the physiological state of individuals during the treatment period. Treatment groups also significantly differed in the diversity of exploratory behaviour. We found that physiological state (body condition, heterophil-to-lymphocyte ratio and oxidative stress) was affected by treatment (Fig 3.), but group differences were best explained by the diversity of exploration of groups, physiological state of individuals improving with increasing group-level diversity of exploration (Fig 4.).

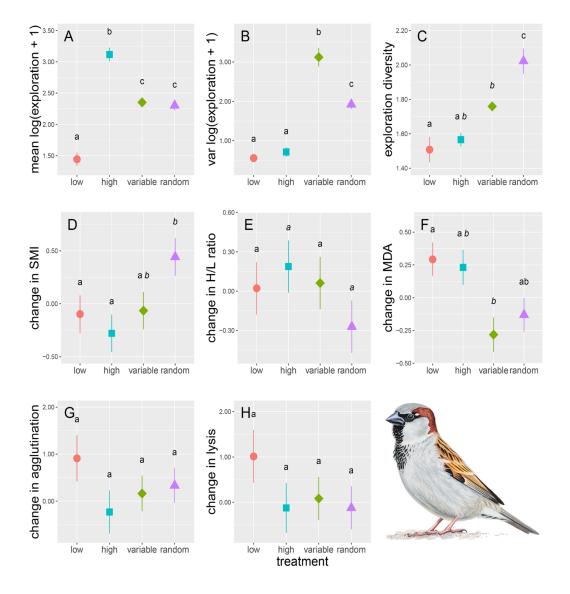


Fig 3. Behavioural and physiological differences among the treatments in social groups of house sparrows (*Passer domesticus*). Treatment groups differ according to (A) mean, (B) variance and (C) Shannon diversity index of personality (i.e. exploration score), change in (D) body condition (SMI), (E) heterophil-to-lymphocyte ratio (H/L

ratio, an indicator of glucocorticoid-mediated stress response), (F) oxidative damage to lipids (i.e. malondialdehyde, MDA), and (G–H) constitutive immune capacity, as expressed through agglutination score (G) and lysis score (H). Means \pm SEM are shown; raw data on panels A–C and model-predicted values on panels D–H. Different lowercase letters denote significant differences (P \leq 0.05), while similar but italicized letters denote marginal differences (P \leq 0.1) between social treatment groups based on pairwise comparisons with Tukey-adjusted P-values. Male house sparrow drawing credit: Márton Zsoldos.

These findings demonstrate that group personality composition affects the condition of group members and individuals benefit from social heterosis (i.e. associating with a diverse set of behavioural types). This aspect of the social life can play a key role in affiliation rules of social animals, in the evolutionary coexistence of different personalities in nature and has implications for human teams and animal welfare.

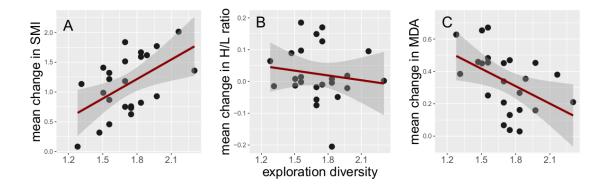


Fig 4. Relationships between personality diversity in social groups of house sparrows (*Passer domesticus*) and mean change in (A) body condition (SMI), (B) heterophil-to-lymphocyte (H/L) ratio, and (C) oxidative damage to lipids (MDA) during the social treatment period. Dots are group-level means, regression lines are model-predicted slopes with 95% confidence intervals (shaded area).

2.8. The effect of groups' personality composition on groups' innovative capacity (Fülöp et al. 2021, in preparation)

How individuals cope with unfamiliar situations is often the key to success in new or changing environments. Acquiring food might require to solve new tasks, hence, individuals have to be innovative, which in turn might be influenced by their personality. In social species, groups can contain individuals with varying phenotypes (e.g. personality). Therefore, group phenotypic composition is expected to be an important aspect determining group functioning, and ultimately success. We experimentally formed groups of house sparrows (*Passer domesticus*) with different personality (i.e. exploratory behaviour) composition in terms of mean and

variance of personality (random, high exploratory, low exploratory and 50% high + 50% low exploratory) and measured the collective innovative capacity of the groups in a novel foraging task. Based on a preliminary analysis of the data, we found no clear differences between treatment groups in their collective innovation. Our results suggest that personality composition of groups in not a primary determinant of the groups' innovative capacity.

3. Further ongoing projects

Besides to the studies presented above, within the frame of the project, we managed to collect additional samples and data, which will be used for further studies, as follows.

3.1. Physiology

From all tree sparrow individuals captured within the frame of the project (N = 420) we prepared a blood smear in order to characterize the cellular innate immunity/inflammation status and physiological stress levels of individuals (see above also study #2.3). Additionally, during three winters (2017/2018, 2018/2019 and 2019/2020) we have collected blood samples from tree sparrows (N = 157) at capture in order to carry out measurements of oxidative stress levels and antioxidant activity. Due to date, all blood smears were counted, and the measurements of redox state variables are planned to be completed soon. Using these data sets, we aim use to study the physiological background of personality and the physiological implications of sociality.

3.2. Malaria

For all tree sparrow individuals (N = 420), from the blood samples collected for molecular sexing, we managed to quantify also infection status (infected or not infected) with malaria blood parasites, and in case of infected individuals, we successfully determined the malaria species and genetic linage present in the samples. Using this malaria data set, we aim use to study potential effects of malaria infection on individual personality, but also potential social transmission pathways of malaria within groups through social networks.

3.3. Kinship analysis

For a subset of tree sparrow individuals (N = 262), for which we have social network data (study #2.4), from the blood samples collected for molecular sexing, we also carried out a microsatellite analysis in order to determine the genetic relatedness (i.e. kinship) between

individuals. Using this data set, we aim to investigate whether kinship is or not a factor influencing social association patterns of individuals during winter.

3.4. Annual survival

Using the data collected during field observations to study the social organization of flocks (study #2.4), and also additional occasional observations on colour-ringed individuals (recorded year-round by volunteers in a dedicated online database: http://openbiomaps.org/projects/pasmon/), we aim to study annual apparent survival of individuals with capure-mark-resighting methods. Specifically, we aim to investigate natural variations in annual survival rates of tree sparrows at our study site, but we also plan to study whether individual phenotypic traits (e.g. sex, physiology, personality) or social features of groups are influencing annual survival or not.

3.5. Aviary study on the relationship between dominance, personality and signalling During February 2020 we carried out an aviary study on tree sparrows to investigate the relationship between individual personality and dominance position, and the status signalling role of the black bib in a controlled environment. At capture, we measured exploratory behaviour of individuals, a measure of individual personality, than we formed two random groups of birds for which we recorded in parallel aggressive interactions between individuals for 12 days. After that, we tested individuals for exploratory behaviour again, and mixed the two flocks. Following another 12 days of recording aggressive interactions between individuals, we made a third set of personality tests and released the birds. Bib size of individuals was also photographed all times when personality tests were made. Data and video materials collected during the study are currently analysed.

4. Deviations

In the project proposal we planned that experimental studies will be carried out on tree sparrow groups temporary held in captivity. However, to study the effect of group personality composition on group functioning, we used the house sparrow as model organism instead of the tree sparrow. The reason for this switch was that tree sparrows are much harder to capture and our local population from where the individuals were planned to be trapped was not large enough for this study. Since the study was carried out in six replicates and on a large sample

size of 240 individuals in total, we decided to choose a model organism with a similar ecology and life-history, but which was available in larger numbers.

5. Publications related to the project

We have also carried out two theoretical investigations of social foraging processes, a topic investigated empirically within the frame of the project as well (see study #2.2). These two theoretical studies were published as two book chapters. The grant K112527 was also acknowledged in a third publication where we investigated a special form of social behaviour, parental care in relation to climatic variables.

5.1. Producer–scrounger models and aspects of natural resource use (Barta 2017, in Giraldeau et al. (eds))

Humans are currently using natural resources at unprecedented rates and it is not difficult to extrapolate how this could lead to global catastrophes of various kinds. To mitigate eventual consequences, our understanding of the processes involved must be improved. Since resource use frequently involves groups, free-riding behaviour (i.e. exploiting the efforts of others) must be expected. Recent evolutionary studies indicate that exploitation of others' efforts can dramatically alter how resources are utilized. Two types of effort are exploitable: the harvesting and maintenance of resources. In this chapter we argue that the exploitation of harvesting efforts can be analysed as a producer-scrounger evolutionary game. The presence of scroungers (exploiters) in a group usually decreases the overall use of resources by the group. Factors that increase the proportion of scroungers (e.g. energy reserves, existence of dominance hierarchy, or prevalence of relatedness) can further decrease resource use. By contrast, aggression and the compatibility of scrounger and producer strategies elevate resource use. In temporally unstable patches, scrounging does not affect resource use in groups that are at equilibrium. Encouraging scrounging may lower resource use, even in humans, but this raises a moral dilemma: individual scrounging is bad, reduced resource overuse by the population is good. Surprisingly, only a small portion of the literature has considered the consequences of cheating in terms of the natural resource management – a situation that demands attention in future research.

5.2. Governance of renewable resources insights from game theory (Valone et al. 2017, in Giraldeau et al. (eds))

Renewable resources have the potential to be used in a sustainable manner but typically are not, often due to the existence of exploiters or free riders. This chapter analyses free-riding behaviour using the prisoner's dilemma-based public goods model and the producer–scrounger model. Overuse of renewable resources is examined under four investor–exploiter scenarios that are derived from modifications of the classic producer–scrounger model, and which vary in the degree of excludability of a discovered resource and in the cost of adopting each strategy. Two important factors are found to reduce overuse: when a finder's advantage can be created for investors, and when the costs of playing exploiter are increased relative to the costs of playing investor. Applying the investor–exploiter model to a fisheries scenario, discussion follows on how interventions designed to reduce overuse may be consistent with the existence of a finder's advantage. A variety of existing interventions can be seen as increasing the costs of adopting the exploiter strategy.

5.3. Parental cooperation in a changing climate: fluctuating environments predict shifts in care division (Vincze et al. 2016, Global Ecology and Biogeography)

It is increasingly recognized that coordinated biparental care is necessary to ensure the survival of offspring in hostile environments, but little is known about the influence of environmental fluctuations on this social behaviour. Assessing the impacts of environmental stochasticity, however, is essential for understanding how populations will respond to climate change and the associated increasing frequencies of extreme weather events. Here we investigate the influence of environmental stochasticity on biparental incubation in a cosmopolitan ground-nesting avian genus. We show that both average ambient temperature and its fluctuations influence parental cooperation during incubation. Male care relative to female care increases with both mean ambient temperature and temperature stochasticity. The degree of flexibility in parental cooperation is likely to mediate the impacts of climate change on the demography and reproductive behaviour of wild animal populations.

6. Conclusions

We carried out a number of studies, in which using both correlative and experimental approaches, we managed to expand our knowledge on the role of individual behavioural differences in the functioning of avian social structures. Furthermore, by collecting a wide spectrum of data about individuals (e.g. physiology, parasitism), phenotypic aspects not

included in our original research plan, we managed to compile additional data sets that have a high scientific potential and open further avenues for research in the future.

During the project period a number of students were involved in the different studies listed above. In total 8 students have completed their BSc thesis and 5 students have completed their MSc thesis successfully.

7. References

7.1. Scientific papers

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7.3. Preprints

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7.4. Manuscripts

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- Fülöp A., Vágási C.I., Osváth G., Pap P.L., Benkő Z., Répás K., Barta Z. The effect of groups' personality composition on groups' innovative capacity.

7.5. Conferences

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