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Individuality and social behaviour

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Individuality and social behaviour

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Part I.

In this part I briefly present the general background of my thesis, followed by a short description of the objectives, methods and main results, and then end by a general discussion and conclusions. An in-depth overview of each specific topic investigated, the complete methodology used in the studies, detailed results and their discussion can be found in the publications listed in Part II of the thesis.

I.1. General introduction

Group-living can be defined as the physical aggregation of individuals belonging to the same species at a certain place and moment, with the conditions that (i) group formation is the result of preferential associations between individuals and (ii) individuals within the group interact socially with each other (Wilson 2000). Hereafter, by individuals, I refer to individuals within the same social group. Interactions among individuals in a group may exhibit a variety of forms (e.g., aggressive encounters, producing-scrounging type social foraging, or leader-follower relationships). Because all aspects of sociality that are observable at the group-level (e.g., dominance relationships, social foraging, collective movement) are based on individual-level interactions, individual interactions may determine the groups' functioning (i.e., performance), and ultimately success (Farine et al. 2015). How group members interact with each other can be influenced by their individual phenotypic traits (e.g,. sex, age, body size, physiology, behaviour) and/or by external conditions (e.g., environmental variables, predation risk, behaviour of other group members). Therefore, individual characteristics can affect group functioning through shaping social processes, but at the same time, group functioning can also retroact on individuals (Farine et al. 2015). Individuals within the group can differ in a series of phenotypic traits, including their behaviour. Consistent individual behavioural differences are conventionally referred to as animal personalities (Réale et al. 2007).

In my thesis I investigate the relationship between individual phenotype with a special emphasis on individual personality, and social behaviour. More specifically, I study how individual differences in phenotype shape different forms of social behaviour and how the social environment (in terms of personality composition of the social group) affects individuals' state.

I.1.1. Individual phenotypic differences

Phenotype describes the set of observable traits of individuals, including (i) morphological and physical characteristics, such as sex, body size or colouration, (ii) developmental and physiological processes like immune capacity or stress responsiveness, and (iii) behavioural traits as personality. Differences among individuals in some of the phenotypic traits are often

evident at first sight (e.g., morphological traits, colouration), yet, other traits (e.g., physiological and behavioural traits) require more complex measurements to reveal them. As such, although the discovery that animals differ in their behaviour was made even in antiquity, the fact that their behaviour is consistently different at individual level, i.e., resembling the personality of humans, was uncovered only recently (e.g., Wilson et al. 1994; reviewed by Gosling 2001). However, as the number of studies investigating the consistency of individual behaviour increased, it became clear that consistent individual behavioural differences are a ubiquitous characteristic of animals including both vertebrates and invertebrates. As a consequence of this discovery animal personality has become one of the central topics of behavioural ecology and evolutionary biology in the last decades. But what is in fact animal personality?

I.1.1.a. Individual personality: definition and categorization

Animal personality (sometimes also termed "temperament"; Réale et al. 2007) is defined as the among-individual differences in behaviour, which are consistent over time and/or across different situations and contexts (Wolf and Weissing 2012). It is important to note, however, that the personality of an individual indicates its position relative to its conspecifics and is not interpreted as the absolute value of a focal behaviour, as measured following a standardized personality test (see below). For instance, according to the definition of personality, an individual that behaves in a certain way at a given time is expected to behave similarly also later and/or if different circumstances, but only in comparison with others. In other words, the behaviour of individuals used to express personality is repeatable, thus variation in behaviour within individual across time and context is smaller than variation in behaviour among individuals at any time or in any context. Thus, personality expresses consistent behavioural differences between individuals from a statistical sample (or population, if the two coincide). Personality also suggests that, although behaviour is considered one of the most flexible phenotypic traits in general (i.e., behavioural plasticity; Dingemanse et al. 2010), its plasticity it can be still constrained within certain limits.

Animal personality traits can be categorized in several ways. According to one of the most widely accepted classification, the so called "Big Five" (Réale et al. 2007), one can distinguish the following five personality

axes: (1) shyness-boldness, indicating an individual's reaction to a risky, but not new situation (e.g., predation); (2) exploration-avoidance, expressing an individual's reaction to a new situation, more specifically its propensity to collect (or avoid collecting) information about something yet unfamiliar to it (e.g., food, environment, etc.); (3) activity, showing the general level of activity of an individual (in a non-risky situation and a non-novel environment); (4) aggressiveness, expressing an individual's tendency to behave agonistically towards conspecifics; and (5) sociability, indicating the level of an individual's attraction towards conspecifics. The latter two axes can only be interpreted in a social context. It has to be noted, that although this classification is more than suitable for a general distinction of the main personality traits, it is not exhaustive. In fact, both the terminology and the methods of quantifying different personality traits lack a general consensus (Carter et al. 2012, Sánchez-Tójar et al. 2022). Thus, some terms were used occasionally as synonyms (e.g., activity and exploration) or the same assay was sometimes used to quantify different personality traits (e.g., novel object test used to measure exploration and boldness; Carter et al. 2012). This lack of unified terminology shows that labelling and measuring different personality traits can be challenging.

I.1.1.b. Quantifying variation in personality

Measuring variation in personality among individuals requires two steps: first, to carry out a standardized behavioural test, and then, to statistically quantify personality based on the data collected during the test. Since personality by definition means consistency in behaviour across time and/or contexts, this requires the repeated testing of at least a subset of the studied individuals (see below) in order to quantify and demonstrate the relative consistency of behaviour.

There are a number of standardized test protocols used to measure variation in personality among individuals, a non-exhaustive list includes the "open-field test", the "novel object test", or the "emergence test" (Carter et al. 2012). The open-field test is one of the most widely used standardized assays to measure the exploratory behaviour of individuals. It is carried out in a novel environment for which the tested individual is naïve, where its behaviour is recorded for a certain amount of time and then the individuals' propensity to

explore the novel environment is quantified (e.g., Dingemanse et al. 2002). Exploratory behaviour can be measured in several ways, for instance by the total number of movements performed during the test period, the proportion of the environment explored during the test, or the time required to explore the whole area of the novel environment. Note that when exploratory behaviour of individuals is expressed using the time required to explore the whole area of the test room, individuals are tested for either until they explore the whole room or until a predefined maximum time period is reached. Individuals which do not explore the whole test room during a maximum time period allocated for the test, usually get a value describing the length of the test as their exploratory behaviour. The use of these measures is arbitrary as there are no widely accepted rules when to prefer one to the other. In many cases, however, most of these measures of exploratory behaviour are strongly correlated with each other. It is important to mention though that if the test rooms used for the open-field tests differ in sizes, the exploration scores found by the above mentioned different methods may not correlate with each other. For instance, in a study on great tits (*Parus major*), Stuber et al. (2013) quantified "exploratory behaviour" both in a small mobile test cage in the field and in a large indoor test room. Although the authors labelled the behaviours they measured in both test arenas as "exploratory behaviour", perhaps for the sake of simplicity, values from the two test arenas were not correlated within individuals. Therefore, the behaviours measured in the two test rooms could mirror different aspects of individuals' personality. To avoid such confusions, in our studies we used two separate terms for the behaviour measured during the open-field test in a small cage and in a large test room as "activity" and "exploratory behaviour", respectively (Studies 1, 2 and 3; see further reasoning in Study 3).

In statistical terms, consistency of behaviour is expressed through statistically significant repeatability (R) of the measured behaviour. Although there are many approaches to calculate repeatability (Nakagawa and Schielzeth 2010, Wolak et al. 2012), the most widely accepted one is the partitioning of the total behavioural variance between among- and within-individual variance components using linear mixed-effects models (LMMs) (Nakagawa and Schielzeth 2010, Dingemanse and Dochtermann 2013, Dingemanse and Wright 2020). With this approach, repeatability is calculated using the following formula:

$$R = V_G / (V_G + V_R),$$

where V_G represents the among-individual variance and V_R the within-individual (or residual) variance (Nakagawa and Schielzeth 2010). LMMs, besides being excellent tools for the partitioning of variance components, are particularly useful in situations when confounding effects (i.e., factors potentially influencing the measured behaviour) have to be also taken into account. Behaviour is one of the most flexible phenotypic traits often influenced by intrinsic and/or extrinsic factors. Therefore, repeatability of the measured behavioural traits in most cases is reported as an "adjusted repeatability", which is a statistically controlled value that incorporates also the variance explained by confounding effects (Nakagawa and Schielzeth 2010).

Repeated testing of individuals for personality is made ideally by running repeated tests for each individual. In practice, however, it is not always possible to carry out repeated personality tests for all individuals, for instance, because not all free-living individuals can be recaptured. A common resolution is to test the repeatability of behaviour on a pooled data set that includes measurements of individuals tested either once or more. It is argued that this pooling improves the precision of the variance estimates. If the studied behaviour turns out to be significantly repeatable, values from individuals measured even only once can then be used in the subsequent statistical analyses that address a biological question.

I.1.1.c. Correlated personality traits

Personality traits are often statistically correlated with each other, forming so-called "behavioural syndromes" (Sih et al. 2004; but see also Garamszegi et al. 2013). A behavioural syndrome thus is a particularity of the sample/population (Bell 2007). Individuals of a sample/population can be characterised by having different behavioural types, indicating a "particular combination of behaviours", as signatures of the behavioural syndrome (Bell 2007).

The proactive-reactive syndrome is often used to characterise individuals' personality. Proactive individuals are considered usually more active, more exploratory, bold, risk-taking, and more aggressive, while reactive individuals are the opposite, they are less active, less exploratory, shy, risk-aversive, and less aggressive (Sih et al. 2004). Proactive individuals are also

more prone to form routines and are more superficial regarding details. In contrast, reactive individuals are more attentive to changes in their environment and adjust their behaviour accordingly, and are thorough in learning details (e.g., Nicolaus et al. 2014).

Besides the covariation of different behavioural traits that form behavioural syndromes, proactive and reactive individuals were found to also markedly differ in their physiology, forming so-called stress "coping styles" (Koolhaas et al. 1999). Accordingly, on the proactive-reactive axis, individuals differ in their response to acute stress as indicated by changes in glucocorticoid stress hormone levels produced by the hypothalamic–pituitary–adrenal axis (HPA axis), one of the principal endocrine regulatory systems: while proactive individuals have a lower stress reactivity (i.e., lower increase of stress hormone levels over a generally lower baseline level), reactive individuals are the opposite (reviewed by Koolhaas et al. 1999, Cockrem 2007). Such differences in physiology are apparent in the immune capacity of individuals as well, but the immune differences between proactive-reactive individuals are less clear (see below). Thus, coping styles are behavioural syndromes extended with a physiological axis.

Recently it was suggested that behavioural types covary with life-history and morphological traits as well, extending the dimensions of the syndromes even further (coined "pace-of-life syndrome", POLS; (Réale et al. 2010, Dammhahn et al. 2018). Hence, according to the POLS hypothesis, individuals characterised by a fast pace-of-life (i.e., that live fast and die young) should prioritize reproduction over survival (i.e., reproduce earlier, have a higher reproductive investment), behave in a more risk-prone way (i.e., be proactive), and invest less in self-maintenance (i.e., have higher metabolic rate, lower HPA axis reactivity to stress stimuli, and lower immune capacity). In contrast, individuals with a slow pace-of-life (i.e., that live slow and die old) should favour survival over reproduction (i.e., reproduce later, have a lower reproductive investment), behave more risk-aversely (i.e., be reactive), and invest more in self-maintenance (i.e., have lower metabolic rate, higher HPA axis reactivity to stress stimuli, and higher immune capacity) (Réale at al. 2010, Laskowski et al. 2021). Studies investigating the relationships predicted by the POLS hypothesis found ambiguous results (e.g., Royauté et al. 2018, Moiron et al. 2020). For this reason, the POLS hypothesis was recently revisited by Laskowski et al. (2021). In their review, Laskowski et al. (2021) recommend

treating behaviour as a mediator of life-history trade-offs in the context of resource allocation-acquisition, rather than an independent causal trait. Also, they suggest that one of the explanations for the lack of consistency in the results of the different studies so far can be that the correlations predicted by POLS might vary at multiple biological levels and depend on the environment (see also Montiglio et al. 2018).

Many studies found relationships between immunity and personality that are often contrasting with what the POLS hypothesis predicts (e.g., proactive individuals had better immunity than reactive individuals; Zylberberg et al. 2014). These results lead to the formulation of an alternative hypothesis, the "risk-of-parasitism" hypothesis, which states that proactive individuals should have a better immunity than reactive ones, because proactive individuals are more exposed to parasites (Barber and Dingemanse 2010), and thus, an up-regulated immunity is favoured by selection for efficiently keeping parasites at bay. Admittedly, the covariation between individual behaviour and immunity can be complex, and it should be interpreted carefully (reviewed by Lopes 2017, McMahon et al. 2022).

To summarize this section, individuals with different personalities are usually characterised by specific behavioural and physiological profiles that seem to be linked to each other and to the life-history strategy of individuals. Consequently, personality can have ecological and evolutionary implications.

I.1.1.d. Ecological and evolutionary implications of individual personality

Personality differences can have wide ranging ecological and evolutionary implications by affecting key biological processes (Wolf and Weissing 2012). For instance, personality can be related to several aspects of reproduction like the expression of different secondary sexual traits (e.g., plumage signals, courtship display, singing activity; Garamszegi et al. 2008; Mateos-Gonzalez and Senar 2012; Naguib et al. 2016, Thys et al. 2020), mate choice (e.g., Teyssier et al. 2014, Chen et al. 2018, Pogány et al. 2018, Sommer-Trembo et al. 2020; but see Laubu et al. 2017) and reproductive success (e.g., Both and Dingemanse 2005, Réale et al. 2009, Mutzel et al. 2013, Patrick and Weimerskirch 2015, Collins et al. 2019; but see McCowan et al. 2015; reviewed by Smith and Blumstein 2008). Furthermore, personality can also be related to dispersal (Dingemanse et al. 2003, Cote et al. 2011, van Overveld et al. 2014)

and survival of individuals (e.g., Santos et al. 2015, Lapiedra et al. 2018, Santicchia et al. 2018; reviewed by Moiron et al. 2020). Consequently, personality may have a strong influence on individual fitness and population demography. Personality can also be an important factor in the spread of parasites and diseases (Barber and Dingemanse 2010), since it may be linked to social dynamics (e.g., social networks; Croft et al. 2009, Aplin et al. 2013, Moyers et al. 2018, López 2020) and individual movement/space use (Aliperti et al. 2021, Wauters et al. 2021). The latter aspect can also be important in colonization of new areas (Liebl and Martin 2012) and invasion processes (Nordberg et al. 2021; see also Chapple et al. 2012), and may also determine the distribution of individuals within habitats (Bonnot et al. 2018, Rabdeau et al. 2021; see also Canestrelli et al. 2016). Hence, personality might be strongly linked to spatial ecology, but also to community ecology and conservation biology.

I.1.2. Group-living: social interactions, their determinants and implications

Group-living implies the preferential association of multiple individuals and the social interactions among them. Interactions between individuals can be of many types, depending on context. For example, while competing for resources (e.g. food, mates), individuals can often engage in agonistic interactions and fight with each other (Hardy and Briffa 2013). In some group-living species agonistic interactions may be used to set up dominant-subordinate hierarchies among group members. Individual group members can divide labour and engage in cooperative interactions while foraging socially (e.g., collective hunting or food gathering), but can also take advantage of other group members and engage in exploitative interactions (e.g., steal food, scrounge). One form of exploitation is the use of scrounging foraging tactic during social foraging (Giraldeau and Caraco 2000). Social interactions are important, since they determine group functioning, and therefore the costs and benefits of sociality. But questions like how are individual phenotypic traits related to the different forms of social interactions and what are their consequences in terms of group functioning are yet poorly understood.

Preferential association of individuals into groups and the various forms of social interactions between them can be accomplished and/or maintained if individuals communicate with each other. Individuals can

communicate through various intraspecific signals, which can be acoustic (e.g. alarm calls, song), visual (e.g., facial expression, body display, colouration) or olfactory (e.g., scent marking). Colour traits are often used for visual signalling and can carry information about their bearers' state, phenotype and/or social status (see below). Therefore, colour traits with a signalling function may mediate social interactions and can determine group functioning by providing information for individuals about their conspecifics. To understand social processes entirely, it is important to study the interactions between individuals, alongside with their appropriate potential signalling mechanisms. For this, we have to explore what the information contents of the different colour traits are (i.e., what capacities they exactly signal) and to assess whether they differ between sexes in species where both males and females possess the same colourful ornament (i.e., mutually ornamented species).

I.1.2.a. Fighting ability and dominance status

Most social groups are organized in linear hierarchies, meaning that some of the individuals have higher social dominance status than others. In these groups, dominant individuals usually have a better fighting ability (also termed "resource-holding potential or power"; Parker 1974, Maynard Smith and Parker 1976) and have priority access to resources, hence occupy higher positions in the groups' dominance hierarchy, as compared to less competitive, subordinate individuals. Since resources are typically limited in nature, dominance status can have important fitness implications for individuals, influencing reproductive success and/or survival (e.g., Ellis 1995, Majolo et al. 2012).

   Dominant-subordinate relationships between individuals are frequently decided during agonistic dyadic interactions. The winner-looser outcome of these interactions usually depends on the fighting ability of contestants. Fighting ability may be determined by several phenotypic traits (e.g., sex, age, and body size; Richner 1989, Briffa 2008, Chamorro-Florescano et al. 2011, Rudin and Briffa 2011, Couchoux et al. 2021). Also, fighting ability and/or dominance status can be related to individual behavioural traits, like personality. Individual personality and fighting ability are expected to be linked because of shared physiological mechanisms as proposed by the POLS hypothesis (e.g., metabolic rate, hormones; Briffa et al. 2015). This expectation is strengthened by the negative frequency-dependent selection, which is

responsible for the maintenance of personality variation and alternative behavioural tactics during competition, also suggesting that a relationship between personality and fighting ability can exist (Briffa et al. 2015). Even though intuitively the relationship between fighting ability and personality seems to be straightforward (e.g., proactive individuals are expected to be more dominant, while reactive individuals mostly subordinate), previous studies found contrasting results (e.g., Dingemanse and de Goede 2004, Cole and Quinn 2012, Rudin and Briffa 2012, Devost et al. 2016, O'Shea et al. 2017, Block et al. 2021). The reasons for these inconsistencies are still unclear, and call for further integrative studies, which consider a number of factors at the same time in order to better understand the relationship between personality and fighting ability and/or social dominance status. We implemented such an approach in **Study 1** in which we studied how a melanin-based colour signal and fighting ability correlate with exploratory behaviour in free-living tree sparrows.

I.1.2.b. Use of producer-scrounger tactics during social foraging

Socially foraging individuals can choose between two alternative foraging tactics: producing (i.e., individuals that actively search for food) and scrounging (i.e., individuals that exploit the findings of the producers by joining them; Barnard and Sibly 1981, Vickery et al. 1991). These two alternative social foraging tactics are widespread across the animal kingdom and their various forms have been reported in both invertebrates (e.g., Dumke et al. 2016) and vertebrates (e.g., Beauchamp and Giraldeau 1997, Barta et al. 2004, Lee and Cowlishaw 2017, Evans et al. 2021).

The use of the producing-scrounging tactics is partly flexible, meaning that individuals can choose at any time which tactic they use to achieve the best foraging efficiency possible given their group mates' behaviour (Giraldeau and Dubois 2008). If no one in the group can increase its foraging efficiency by switching tactic, the group is settled in a state of equilibrium in terms of social roles (Giraldeau and Caraco 2000). In other words, tactic use in this equilibrium state represents an evolutionary stable strategy (ESS). Foraging tactic use has been the subject of a large body of theoretical studies, in which stable tactic use was investigated in game-theoretical models (Giraldeau and Caraco 2000). Later, model predictions were investigated empirically

(Giraldeau and Dubois 2008), and as a consequence, tactic use has been shown to be influenced by individuals' phenotype, e.g., sex, energy reserves, dominance status, or personality (e.g., Liker and Barta 2002, Lendvai et al. 2004, 2006, Kurvers et al. 2010, David and Giraldeau 2011, Aplin and Morand-Ferron 2017). Group characteristics (e.g., size, composition and/or geometry; Coolen 2002, Mónus and Barta 2008, Tóth et al. 2009, Alfaro and Cabrera 2021) or predation (Barta et al. 2004) were also shown to affect foraging tactic use.

Social foraging tactic use is flexible only to a certain level. Interestingly, some studies found that individuals tend to use tactics consistently, that is, some individuals are mostly producers, while others are mostly scroungers (Beauchamp 2001, Keynan et al. 2015, Aplin and Morand-Ferron 2017). Consistency in social foraging tactic use resembles personality, and indeed, based on the POLS hypothesis, proactive-reactive individuals are expected to play alternative behavioural strategies when foraging socially. Besides, similarly to fighting ability (see above), negative frequency-dependent selection can be a common evolutionary mechanism maintaining behavioural variation in personality and social foraging tactic use as well, suggesting a link between the two behaviours. More specifically, since scrounging assures a faster benefit (Wu and Giraldeau 2005), one would expect proactive individuals with a higher metabolic rate to scrounge more and reactive individuals with a lower metabolic rate to produce more. Alternatively, since producing is the more risk-prone tactic and requires more exploration (Wu and Giraldeau 2005), one would expect proactive individuals to produce more and reactive ones to scrounge more. Previous studies found a connection between social foraging tactic use and personality (e.g., Kurvers et al. 2010, David et al. 2011, Jolles et al. 2013; but see Aplin and Morand-Ferron 2017), yet, the direction of the association varied between studies. The apparent differences between the results published so far emphasizes the need for further research in order to unravel the relationship between these two forms of behaviour and the factors shaping the direction of the relationship. In **Study 2** we address this question using data on free-living tree sparrows.

I.1.2.c. Intraspecific colour signalling

Conspicuous colour traits represent a widespread form of visual signalling in the animal kingdom and are used in various situations. In group-living species, for instance, status of individuals in the dominance hierarchy is often signalled toward conspecifics through conspicuous colour patches (e.g., so-called "badges of status"). In this respect, colour signals serving as badges of status have the primary function to mediate conflicts between group members by indicating the competitive ability of the individuals. Therefore, badges of status can provide a clue for individuals whether to engage or not in agonistic interactions based on mutual assessment of fighting ability (Arnott and Elwood 2009, Elwood and Arnott 2012, Fawcett and Mowles 2013; but see Pinto et al. 2019). Besides functioning as badges of status, colour traits can also signal other qualities/phenotypic traits of individuals (e.g., body condition, immune capacity, oxidative stress, parasite load, behaviour; reviewed by e.g., Svensson and Wong 2011, Pérez-Rodríguez et al. 2017, San-Jose and Roulin 2018).

Colour traits can be achieved by individuals via three modalities: (i) pigment molecules, (ii) specialized integument structures (i.e., structural colouration), or (iii) the combination of the two. Carotenoids, responsible for the yellow-orange-red-pink colouration, and melanins (i.e., pheomelanin and eumelanin), responsible for the grey-brown-black colouration, are the two main pigment molecules that make up the colouration of most of the bird and mammal species. Carotenoids cannot be synthesized by animals and hence must be acquired through the diet. In contrast, melanins are produced by organisms from amino acid precursors (e.g., tyrosine) through a process called melanogenesis. This process is relatively conserved from an evolutionary point of view and is similar in both invertebrates and vertebrates (San-Jose and Roulin 2018). Melanin synthesis is orchestrated by the melanocortin system which involves genes with pleiotropic effects and several receptors of melanocortins (i.e., peptide hormones involved in melanin synthesis) located in various tissues and cells of the body (e.g., skin, reproductive organs, immune cells; Ducrest et al. 2008). Hence, as the melanocortin system is connected among others to systems responsible for colouration, energy homeostasis, immunity, stress response and behaviour, one may expect eumelanic colouration to be related to phenotypic traits regulated by the melanocortin system. According to the melanocortin hypothesis, individuals with more pronounced eumelanin-based signals should have higher metabolic rate, larger body size, better anti-inflammatory immune capacity, should be less sensitive to

stress, and should be more aggressive (i.e., more dominant) (Ducrest et al. 2008, San-Jose and Roulin 2018). Therefore, one would expect more eumelanic individuals to be proactive, while less eumelanic individuals to be reactive. Melanin-based colouration was thoroughly investigated and a large body of evidence supports these predicted associations between the expression of various melanin-based colour traits and individual phenotype, though exceptions also exist (reviewed by Ducrest et al. 2008, San-Jose and Roulin 2018). For instance, the status signalling function of conspicuous colour traits was studied in some well-known model species (e.g., house sparrow *Passer domesticus*; reviewed by Sánchez-Tojár et al. 2018), yet, in other species a similar function of conspicuous colour traits is still poorly explored. This is especially true for species with reduced or no sexual dimorphism (e.g. Eurasian tree sparrow *Passer montanus*), in which ornamental traits are present in both sexes and might have a sex-specific signalling function, hence can affect social processes in a sex-dependent manner. The same reasoning applies to other traits linked to melanin-based colouration (e.g., immunity, personality) that were previously investigated without considering the potential confounding effect of sex (but see e.g., Fargallo et al. 2014). Thus, the sex-specific signalling function of melanin-based conspicuous colour traits in (apparently) sexually monomorphic species requires further investigation. We designed **Studies 1 and 3** to fill these gaps in our knowledge using free-living tree sparrows.

I.1.3. Phenotypic composition of groups: group functioning and its feedback to individuals

As we have seen, individuals can often differ in their phenotype (e.g., sex, age, body size, colouration, physiology, behaviour). Consequently, groups usually consist of individuals with different phenotypes ("group phenotypic composition", GPC; Farine et al. 2015). GPC can be captured (statistically) by the distribution of phenotypes in the group and hence can be characterised by various statistics, expressing different aspects of groups' composition: mean (e.g., lower or higher average age) and/or variance of phenotypes (e.g., lower or higher variance of body size), the diversity of phenotypes (e.g., lower or higher Shannon diversity of individual stress responses), or the shape of distribution of phenotypes (i.e., frequency of different types of phenotypes; e.g. normal, uniform or skewed distribution of individuals with different bold-shy

personality) in the group (Farine et al. 2015). Also, groups can differ either in only one of the measures listed above (e.g., they have different means, but similar variance), or in multiple measures at the same time (e.g., they have both different means and variances).

GPC can have a strong influence on group functioning and group performance through influencing social interactions among group members (Jolles et al. 2017, 2020). Furthermore, group performance in turn is expected to carry consequences on individuals through determining individual's fitness (Farine et al. 2015). Hence, individual phenotype and group performance are linked to each other in a bidirectional way, creating a feed-back loop: an "upstream" effect (i.e., the effect of individuals on group performance) and a "downstream" effect (i.e., the effect of group performance on individuals). It is still unclear how GPC affects group-level processes (e.g., dominant-subordinate relationships, social foraging, intraspecific communication) and how group performance affects individuals of the group in terms of their condition or physiology (Loftus et al. 2021). According to a recent review (Loftus et al. 2021), the general pattern of the upstream effect is that groups with a more heterogeneous, more variable composition perform better. Interestingly, the downstream effect of GPC on individuals was seldom investigated (Farine et al. 2015, Loftus et al. 2021).

Among the first physiological responses to any stressful stimuli (e.g., increased intra-group competition, low foraging efficiency) is the activation of the HPA axis, which, among other things, coordinates glucocorticoid hormone production and plays an important role in an otherwise complex stress response (reviewed by Sapolsky et al. 2000). This stress response is accompanied by changes in body condition, and/or markers of immunity and oxidative stress. If the stressor persists (chronic stress), these markers on inner state can suffer long-lasting changes (Martin 2009). Therefore, the well-being of individuals in different social environments (i.e., groups with different GPC) is supposedly reflected by their physiological state. Intriguingly, this question has never been investigated. We aimed to study this fundamental biological question by experimentally stetting different GPCs based on the exploratory behaviour of house sparrows held in captivity (**Study 4**).

I.2. Objectives, methods and major results

Study 1. Fülöp et al. (2022) Fighting ability, personality and melanin signalling in free-living Eurasian tree sparrows (*Passer montanus*). (submitted manuscript)

(i) Objectives

Individual fighting ability, a primary determinant of dominance status, is expected to be influenced by certain aspects of individuals' phenotype, including sex, morphological characteristics (e.g., body size) and behaviour (e.g., personality). Apparently the relationships between fighting ability and these phenotypic traits of individuals are not always straightforward, potentially being species-specific or shaped by external factors (e.g., context, group composition). Also, individual fighting ability is often communicated towards conspecifics through ornamental traits. This status signalling function of ornamental traits is already known in many species, but in other species as the Eurasian tree sparrow, the function of such traits is less known. **In this study we aimed to investigate the relationship between fighting ability and individual personality (i.e., exploratory behaviour), and the status signalling function of the black throat patch (i.e., bib) in free-living tree sparrows, with respect to sex and body size.**

(ii) Methods

We have captured 194 tree sparrows during three wintering seasons, between 2013 and 2016. At capture, we marked all birds with an individual combination of colour rings, collected a small blood sample for genetic sex determination, and data about the individuals' body mass, tarsus length, wing length, bib size (i.e., area) and exploratory behaviour. Exploratory behaviour of individuals was quantified using the open-field test in a large test room serving as a novel environment. Birds were then released at the site of their capture. We recorded the agonistic behaviour of 32 marked individuals on bird feeders while foraging in groups during multiple foraging bouts after their release. We characterised fighting ability using probability of winning a fight as a proxy.

(iii) Results

We found no difference between sexes in the probability of winning, and probability of winning was not predicted by exploratory behaviour or body size in none of the two sexes. However, probability of winning was sex-dependently related to bib size: in females bib size was positively correlated with probability of winning a fight, while in males this association was not significant.

Study 2. Fülöp et al. (2019) Personality and social foraging tactic use in free-living Eurasian tree sparrows (*Passer montanus*). *Behavioral Ecology* 30(4): 894–903. DOI: https://doi.org/10.1093/beheco/arz026

(i) Objectives
Social foraging tactic use (i.e., producing or scrounging) is often phenotype-related. As previous studies show, the use of producing-scrounging tactics can also be sex-dependent and determined by the individuals' dominance status or personality. Moreover, the connection between individual phenotype and social foraging tactic use might also be influenced by various external factors (e.g., group size and/or density, predation risk) and these potentially confounding factors could be the cause of the inconsistencies between the previous results. **In this study we aimed to investigate the relationship between the use of producing-scrounging tactics and individual personality (i.e., exploratory behaviour) in free-living Eurasian tree sparrows, accounting for sex and dominance status of individuals.**

(ii) Methods
We have captured 194 tree sparrows during three wintering seasons, between 2013 and 2016. At capture, we marked all birds with an individual combination of colour rings, collected a blood sample for genetic sex determination, and data about the individuals' body mass, tarsus length, wing length, bib size (i.e., area) and exploratory behaviour. Exploratory behaviour of individuals was quantified using the open-field test in a large test room serving as a novel environment. Birds were then released at the site of their capture. We recorded the use of the producing-scrounging foraging tactics of 37 marked individuals after their release on special bird feeders, which simulated the patchy distribution of food, and during multiple foraging bouts.

(iii) Results

We found no difference between sexes in social foraging tactic use (i.e., probability of scrounging) and bib size (i.e., a proxy of dominance status) was not related to tactic use in either sex. Yet, we found that social foraging tactic use was sex-dependently correlated with exploratory behaviour: while more exploratory females scrounged more, exploratory behaviour was not associated with foraging tactic use in males. Furthermore, the density of foraging individuals and time of the feeding event within the foraging bout were both significantly positively related to probability of scrounging, independently of sex.

Study 3. Fülöp et al. (2021) Sex-specific signalling of individual personality by a mutual plumage ornament in a passerine. *Behavioral Ecology and Sociobiology* 75: 38. DOI: https://doi.org/10.1007/s00265-021-02971-z

(i) Objectives
The function of conspicuous colour traits was mostly investigated in sexually dimorphic species in which only one sex possesses the coloured signal. In many species, however, conspicuous colourful traits are possessed and used as signals by both sexes (i.e., mutually ornamented species). In such species the signalling function of conspicuous colour traits can have similar or different functions in males and females. Yet, this question has been seldom studied. **In this study we aimed to investigate the signalling function of a mutual melanin-based plumage ornament, the black throat patch (i.e., bib) of Eurasian tree sparrows, while accounting for the effects of sex and body size.**

(ii) Methods
We studied the relationships between bib size (i.e., area) and body condition (i.e., size-corrected 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) during four wintering seasons, between 2016 and 2020. We have captured 199 free-living tree sparrow individuals at bird feeders and collected a blood sample for genetic sex determination and leucocyte profiling, and data about the individuals' body mass, tarsus length, wing length, bib size and activity. Activity of individuals was quantified using a field-adapted version of the open

field test in a small size mobile test arena. After processing, we released the birds at the site of their capture.

(iii) Results

We found that bib size was significantly larger in males than females; and was not related to body size in any of the two sexes. Bib size was sex-dependently associated with activity: bib size was negatively associated with activity in males and positively in females. Furthermore, bib size was positively related to physiological stress levels (i.e., ratio of heterophils to lymphocytes), independently of sex, but was not associated with body condition and cellular innate immunity/inflammation status (i.e., total leucocyte counts) of individuals.

Study 4. Vágási C.I.* and Fülöp A.* et al. (2021) Social groups with diverse personalities mitigate physiological stress in a songbird. *Proceedings of the Royal Society B: Biological Sciences* 288(1943): 20203092. DOI: https://doi.org/10.1098/rspb.2020.3092 (*shared first authorship)

(i) Objectives

Phenotypic composition of groups is known to affect group-level social processes and performance. The other way around, emergent group-level properties are also expected to influence the state and/or fitness of group members. This latter aspect of sociality is, however, largely unexplored. **In this study we aimed to investigate the effect of groups' personality composition on the physiological state of group members.**

(ii) Methods

We established experimental groups of wild-caught house sparrows with different personality composition (described through the mean, variance and Shannon diversity of exploration) and tested the effect of group composition (i.e., social environment) on the physiological state of group members. We quantified exploratory behaviour of individuals using the open-field test in a large test room serving as a novel environment, and we characterised physiological state by the body condition (i.e., size-corrected body mass), chronic physiological stress levels (expressed through the ratio of heterophils to lymphocytes), oxidative stress levels (expressed through the malondialdehyde

concentration) and two measures of innate immunity characterising natural antibody activity (expressed through the agglutination score) and complement system activity (expressed through the lysis score).

(iii) Results

We found that individuals from groups with a higher group-level exploration diversity had better body condition and lower levels of chronic and oxidative stress than individuals from groups with lower group-level exploration diversity, independently from the individuals' sex and personality. The two measures of innate immunity were not affected by the experimental social treatment either alone or in interaction with individual's sex or personality.

I.3. General discussion and conclusions

Social behaviour is a truly complex phenomenon. On one hand, it has diverse forms of manifestation, each being the outcome of specific interaction between individuals. Social interactions between individuals determine group-level performance, which in turn is expected to influence the individuals themselves. Social interactions between individuals are determined by the phenotype of individual group members. Hence, individual phenotype influences group functioning and performance (i.e., upstream effect), while group performance affects individuals through a feed-back loop (i.e., downstream effect) (Farine et al. 2015). My thesis is centred on the relationships between individual differences in phenotype and group-level processes; and on the feedback of the latter on individuals. Accordingly, my aims were two-fold: (1) to determine how individual phenotype, especially individual personality, is associated with the different aspects of sociality and (2) to unravel how emerging group-level characteristics (i.e., phenotypic composition of groups), originating from the personality differences between individuals, are affecting individual group members. To achieve these two aims, we investigated social behaviour in two highly social sparrow species, the tree sparrow and the house sparrow, both under natural conditions and captivity, using correlative and experimental approaches as well.

I.3.1. From individuals to groups
We studied by correlative means the upstream links between individual phenotype and two aspects of group-level social behaviour in free-living tree sparrows, social dominance and social foraging. Besides, we also investigated intraspecific colour signalling, which is a potential mediator of these social interactions. We found that fighting ability, a determinant of social dominance, was not predicted by sex or exploratory behaviour of individuals (Study 1). However, the probability of scrounging during social foraging was positively related to exploratory behaviour in females, but not in males (Study 2). Additionally, probability of scrounging was not related to bib size (a trait being used in this study as a proxy of dominance status; Torda et al. 2004, Mónus et al. 2017; see also Study 1) independent of sex. Bib size of individuals was related to sex, as bib size of males was larger than those of females (Study 3; see also Mónus et al. 2011). Bib size was also sex-dependently related to

fighting ability: positively in females, but non-significantly in males (Study 1). Bib size was also sex-dependently related to activity: negatively in males, while positively in females (Study 3). Furthermore, bib size was positively related to physiological stress levels (i.e., ratio of heterophils to lymphocytes) in both sexes (Study 3).

In this section I will focus on discussing the results on fighting ability and social foraging tactic use, a detailed discussion about bib size can be found in the next section. Both forms of social interactions are expected to be associated with individual personality based on the POLS hypothesis, which predicts that proactive individuals with a fast pace-of-life should have superior fighting ability and should scrounge more because they invest more into resource acquisition and not allocation (Laskowski et al. 2021). Thus, the lack of relationship between fighting ability and exploratory behaviour (Study 1) does not support the POLS hypothesis. Our findings for social foraging tactic use do confirm an association between probability of scrounging and exploratory behaviour, but in only one of the sexes (Study 2). One potential explanation for the mismatch between our findings and predictions of the POLS hypothesis is that the associations predicted by POLS could remain masked if they were influenced by environmental factors, as suggested by Laskowski et al. (2021). Which environmental factors exactly can determine the investigated relationships remains an open question.

There is no overall agreement among studies that investigated these associations either. A couple of non-exclusive explanations can be formulated for why these relationships are apparently so labile. Firstly, behaviour is among the most plastic phenotypic traits. Even though behavioural traits can be repeatable within individuals (e.g., personality traits), there is still a large amount of plasticity in behaviour. The average repeatability for personality traits is around 0.35 (Bell et al. 2009), so there is plenty room for plastic adjustments. This plasticity can then easily influence associations between different behavioural traits (e.g., personality, agonistic behaviour, producer-scrounger tactic use). Secondly, there is a large variation between studies in the setup they used (e.g., captivity vs. natural conditions), the personality traits they investigated (e.g., exploratory behaviour, boldness), and in quantifying fighting ability/dominance and social foraging tactic use. These inconsistencies could also result in differences between reported findings. Finally, the relationships can be species-specific, as species widely differ in their social systems (e.g.,

group size: small vs. large; group dynamics: fission-fusion vs. stable; dominance structure: egalitarian with no hierarchy vs. despotic with a strong linear hierarchy). All these factors can determine the studied associations, and hence, may contribute to the inconsistencies we observe in the results of published studies.

In sum, our results suggest that individual differences in personality can potentially affect certain group-level processes through shaping social interactions (e.g., producing-scrounging social foraging tactics). However, the fact that for most of the investigated relationships we couldn't confirm the predicted associations, emphasize the necessity for further investigations conducted under diverse but controlled circumstances.

I.3.2. Can bib size be a mediator of social interactions?

In order to understand the black bibs' potential role as a mediator of social interactions in tree sparrows, its function should be determined in the first place. Despite the relative ubiquity and large distribution range of the tree sparrow, this species was rarely investigated and, hence, our knowledge on the signalling role of the bib is limited. Interestingly, the closely related house sparrow has become one of the primary model organisms for the investigation of the signalling function of eumelanin-based badges of status (Sánchez-Tojár et al. 2018). In tree sparrows, the signalling function of the bib has been studied exclusively by correlative approaches with studies reporting a series of contrasting results. The status signalling function of the bib is the most "thoroughly" investigated, being addressed by three studies (Torda et al. 2004, Mónus et al. 2017, Study 1). Torda et al. (2004), having no knowledge on the individuals' sex, found that the dominance status of individuals was positively correlated with bib size in some of the captive groups, but not in the others. Mónus et al. (2017) found in free-living individuals that bib size was positively associated with fighting ability in males, but not females. Our Study 1 used a similar setup to Mónus et al. (2017), and we found the diametrically opposed relationship. Overall, the results of these three studies can be interpreted in two ways. Firstly, bib size can function as a status signal in tree sparrows, but the relationship between bib size and status may be confounded by intrinsic or extrinsic factors, leading to this large heterogeneity in the results. Secondly, these contrasting results can also mean that the correlation between bib size and status is very weak and is only occurring by chance in some cases and/or under

certain circumstances. The status signalling of the black throat patch in male house sparrows has been recently questioned as well after re-analysing several case studies in a meta-analysis (Sánchez-Tojár et al. 2018). According to the current state of the art, there is more evidence for the sexual signalling, rather that status signalling, role of the black throat patch in house sparrows, as patch size was not related to dominance status in most of the studies, but has been found to be related to aspects of reproduction (e.g., mate choice; Møller 1988, Møller 1989; but see Kimball 1996) and fitness (e.g., Jensen et al. 2004). Hence, at least in house sparrows, this trait seems to be an honest indicator of male genetic quality. Note that, good quality males can be better competitors as well, which can explain the occasionally found correlation between throat patch size and status. In tree sparrows no studies have investigated the role of bib size in the context of reproduction or the relationship between bib size and fitness. These questions would be especially interesting to study in tree sparrows (or in any other mutually ornamented species) in relation with sex because males and females bear the same ornament, which can have a similar or sex-specific signalling role.

Bib size was also associated with sex, the activity axis of personality and with chronic physiological stress levels (i.e., ratio of heterophils to lymphocytes) (Study 3). It has to be mentioned here that the personality trait we labelled "activity" is presumed to reflect the behavioural response of individuals to a risky life event (i.e., trapping and handling), as the test was performed right after capture. Hence, activity of individuals is expected to mirror acute stress, mediated by the HPA axis (e.g., Martins et al. 2007; Baugh et al. 2013; but see Baugh et al. 2012). The adaptive value of the elevated glucocorticoid levels is, on the one hand, the sparing of glucose stores by shutting down energy-demanding functions (e.g., reproduction, growth), and on the other hand, mobilizing glucose reserves to serve survival in a stressful situation (e.g., increase activity, escape behaviour; Sapolsky et al. 2000). Therefore, reactive individuals with a higher glucocorticoid stress reactivity are expected to become more active in response to acute stress, hence their activity levels should increase. In contrast, proactive individuals with a low glucocorticoid stress reactivity should maintain or eventually increase their activity level, but to a lesser extent than reactive individuals. Note, however, that the behavioural reaction of proactive-reactive individuals to a risky situation can depend on multiple factors (e.g., risk assessment), which might

influence the way how individuals will react (e.g., Quinn and Cresswell 2005). A potential link between eumelanin-based colouration, physiology and behaviour is provided by the melanocortin system (Ducrest et al. 2008). Due to the pleiotropic effects of the genes regulating melanin synthesis, eumelanin-based colouration should covary, among others, with energy homeostasis, glucocorticoid stress reactivity, immunity, and behaviour. In general, more eumelanised individuals should have a more optimal balance between energy intake and expenditure, be more resistant to acute stress, have higher immune potential, and should be more aggressive (Ducrest et al. 2008, San-Jose and Roulin 2018). Our correlative results bring only a weak support for the melanocortin hypothesis. There might be a couple of potential explanations for this weak support. Firstly, our study is correlative with a cross-sectional sampling approach, meaning that the associations we described represent a snapshot about the sample. Systematic, repeated measurements of individuals would definitely strengthen the conclusions we could draw from our results. Note that some of the variables we measured can be best interpreted in the context of the melanocortin hypothesis when compared to a baseline level (i.e., quantifying the change in body mass, cellular immunity, glucocorticoid levels). Repeated measurements also have the advantage to give a more representative characterization of individuals, especially when measuring traits with high plasticity like activity under acute stress exposure. Secondly, the melanocortin hypothesis may not be the only framework explaining associations between eumelanin-based colouration and phenotype, as several studies found no connection between eumelanin-based colouration and melanocortin gene expression or coding sequence variation (e.g., Riyahi et al. 2015, Corti et al. 2018). These studies suggest that other mechanisms can be also responsible for the covariation between eumelanin-based colouration and phenotype. Experimental studies are necessary for a deeper insight into the associations we investigated.

In summary, the black bib of tree sparrows may signal multiple aspects of individuals' phenotype including sex, physiological state and behaviour. Yet, the mechanistic links between bib size and phenotypic traits are unclear. Nevertheless, these results suggest that bib size can function as a potential mediator of social interactions; and also, colour signalling appears to be an important form of communication between individuals in this species. There are, however, many questions left open about the function(s) of the black

bib in tree sparrows. Future studies should investigate the function of the bib experimentally (or in a controlled environment) and should focus on (i) the role of the bib in individual recognition, (ii) the signalling function of the bib during the breeding and non-breeding seasons, thus across multiple contexts, (iii) the mechanistic links between bib size and phenotype, (iv) the selective forces maintaining variation in bib size and its' heritability, and (v) the colour characteristics (i.e. brightness) of this ornament.

I.3.3. Sex-dependent associations in tree sparrows

Many of the associations between phenotypic and/or behavioural traits investigated in tree sparrows were sex-dependent (e.g., body condition vs. activity, bib size vs. activity, fighting ability vs. bib size, exploratory behaviour vs. social foraging tactic use; Studies 1, 2 and 3). These results suggest an important role of sex in shaping either phenotypic correlations (i.e., phenotypic integration of traits; Pigliucci and Preston 2004) and/or social processes in this species. These results are especially interesting when considering that tree sparrows exhibit only a very weak sexual size dimorphism, males being only slightly bigger than females with considerable overlap in the morphological trait ranges of the sexes (Mónus et al. 2011, Study 3). Males and females look similar to the human eye in terms of colouration as well, but a study reported sexual dichromatism using reflectance spectra (Eaton 2005). Also, note that our studies were performed during the wintering stage of the annual cycle, when the hormonal differences between males and females are presumably less pronounced, as compared with the breeding season. But how can sex be such a central element in shaping trait correlations during the non-breeding period? In a social context, for example, sexes might use alternative strategies to acquire resources (e.g., sex-specific foraging strategies). Intersexual competition for resources has been suggested to drive evolution of sexual dimorphism in morphology, behaviour, etc. through differential use of ecological niches by males and females (Li and Kokko 2021). This can result in eventual sex-specific trait correlations. Nevertheless, the causes and the consequences of this phenomenon are still unclear and this topic could be a prospective avenue for future investigations.

I.3.4. From groups to individuals

We have studied experimentally the downstream effect of group personality composition on individual physiological state in captive house sparrows. We found that a more diverse group personality had more beneficial effects on the physiological state of individuals than a more uniform one (Study 4). The measured effect of groups' personality composition on individual state was the same for all individuals, independently of their phenotype (i.e., sex, personality), meaning that all individuals benefited equally from the behavioural diversity of the group. These results suggest that groups with different personality composition function differently (i.e., may differ in their performance) and this ultimately affects the physiological state of individuals in these different groups. But what is "performance" exactly in this context? In free-living groups performance can be measured, for instance, in foraging success or predator avoidance, both determining individual fitness. In our aviary experiment, food shortage and predation were excluded because individuals were held in captivity throughout the experiment. Moreover, individuals were housed indoor at a constant room temperature well above the outside temperature which is a very favourable condition during the winter. Despite these benign ecological conditions experienced in captivity, we found detectable differences in the individuals' physiological state between the treatment groups after a short treatment period of only nine days. As we didn't measure group performance directly in our experiment, we can only speculate on the causes that resulted in the differences we found. In the literature there are several non-exclusive explanations proposed regarding why diverse groups can perform better (reviewed by Farine et al. 2015, Loftus et al. 2021). Firstly, diverse groups more likely contain individuals with different skills or which are specialized to some tasks. Secondly, keystone individuals, which have a disproportionally higher effect on group functioning than other individuals and which can direct group behaviour, can occur with a higher probability in diverse groups (see also Modlmeier et al. 2014). Thirdly, the complementarity effect between individuals with different phenotypes (e.g., personality) can be more pronounced in diverse groups. Nevertheless, we should be careful in generalizing these findings, for multiple reasons. Firstly, it is hard to tell whether these effects are the same in free-living groups as in captive groups, since ecological conditions are markedly different in the two circumstances, potentially influencing social processes. Secondly, these effects are not necessarily universal for all species. Social systems can be strikingly different

across species, hence, we can expect significant species-specificity in the effects we found. Overall, the exact social mechanisms of how group personality composition is affecting group functioning and performance definitely need some more clarification. Thus, further studies (i) should investigate the effect of GPC on the occurrence and distribution of roles (e.g., leader-follower, producer-scrounger, innovators-non-innovators, keystone individuals) within the groups, and (ii) the effect of GPC on the type and frequency of the different social interactions (e.g., dominance interactions) between group members. Research is also needed to unravel the ultimate fitness consequences of GPC.

I.3.5. Conclusions

It is not easy to fit all the results presented in this thesis into an overall, general picture. I can conclude, though, that individual phenotypic differences, especially sex and personality, can influence aspects of sociality, such as social foraging and intraspecific communication (i.e., signalling), in group-living animals. Therefore, individual phenotypic traits are important contributors to the functioning and performance of social groups (i.e., upstream effect). In turn, performance of groups with different phenotypic composition seems to influence the physiological state of individual group members (i.e., downstream effect). The mechanisms of how individual phenotypic traits determine group-level performance, and how group-level performance feeds back on group members still have to be elucidated.

I.4. Összefoglaló (summary in Hungarian)

A szociális életforma, legyen az időszakos vagy állandó, az egyedek csoportokba való szerveződését feltételezi, mely egyazon fajhoz tartozó egyedek fizikai tömörülését jelenti, azzal a feltétellel, hogy az (i) az egyedek aktív döntése következtében alakuljon ki, illetve (ii) az egyedek a fajtársaikkal szociális interakciókat alakítanak ki (Wilson 2000). Csapatos viselkedés során az egyedek különféle interakciókat alakíthatnak ki egymással, ilyenek például az agresszív összetűzések, amelyek a csapaton belüli dominancia viszonyok tisztázásához szükségesek, a szociális táplálkozás során a kereső-potyázó taktikák használata, vagy épp a vezető-követő kapcsolatok. A felsorolt interakciók, de nem csak kizárólag ezek, olyan egyedi viselkedésbeli megnyilvánulások, amelyeket mind az egyedek fenotípusos jellegei (pl. ivar, kor, testméret), mind a külső körülmények (pl. klimatikus viszonyok, predációs kockázat, fajtársak viselkedése) befolyásolnak. Ezen egyedi szintű interakciókon alapul a csoport szinten kialakuló szociális viselkedés valamennyi aspektusa (pl. dominancia viszonyok, szociális táplálkozás, intraspecifikus kommunikáció) amelyek meghatározzák a csoport együttes működését, majd végső soron sikerességét. Az egyedek tulajdonságai tehát hatással vannak a szociális folyamatok alakítása révén a csoport működésére, de ugyanakkor, a csoport működése (a sikeressége által) visszahathat az egyedekre (Farine és mtsai. 2015). Az egyedek nem egyformák, számos fenotípusos jellegben, így viselkedésükben is, különböznek. A konzisztens egyedi viselkedésbeli különbségeket egyezményesen állati személyiségnek nevezzük (Réale és mtsai. 2007). Értekezésem központi témája az egyedi személyiség és a szociális viselkedés közötti kapcsolat vizsgálata. Pontosabban, hogyan befolyásolja az egyedek személyiségbeli különbözősége a szociális viselkedés különféle formáit, illetve hogyan hat a szociális környezet (a személyiség összetétel szempontjából) az egyedekre. Ezen kérdéskört járja körbe a lentebb röviden ismertetett négy esettanulmány.

1. vizsgálat. Fülöp és mtsai. (2022) Kompetitív képesség, személyiség és melanin alapú tollazati jelzések szabadon élő mezei verebeknél (*Passer montanus*). (beküldött kézirat)

Az erőforrások jellemzően korlátozottan fordulnak elő a természetben, ezért elérhetőségük fitnesz következményekkel jár az egyedek számára. A csapatokban élő egyedek erőforrásokhoz való hozzáférése gyakran agresszív összetűzések során dől el, amelyek kimenetelét a résztvevők kompetitív képessége határozza meg. Az egyedek kompetitív képessége összefüggésbe hozható számos egyedi fenotípusos jelleggel, ilyenek például az ivar, kor, vagy testméret. Egy másik jelleg, amit szintén gyakran összefüggésbe hoztak a kompetitív képességgel, az egyedek személyisége. Eddigi ismereteink alapján azonban a személyiség és a kompetitív képesség közötti kapcsolat korántsem tisztázott. Az egyedek kompetitív képességüket fajtársaik felé gyakran különféle színezetbeli jellegekkel közvetítik. Ezen jellegek szerepe sok faj esetében tisztázott, másoknál viszont kevésbé. Vizsgálatunkban, az ivarra és a testméretre kontrollálva, az egyedek felfedező viselkedése és kompetitív képessége közötti kapcsolatot kutattuk szabadon élő mezei verebeknél (*Passer montanus*) két téli időszak alatt, szociális táplálkozás alatt. Vizsgáltuk továbbá az egyedek fekete torokfoltjának – amely egy eumelanin alapú tollazati jelleg – státusz jelző szerepét, hímekben és tojókban egyaránt. Az egyedek kompetitív képességét, amelyet a nyerési valószínűséggel jellemeztünk, nem prediktálta a felfedező viselkedés vagy a testméret. Az egyedek torokfoltja ivar-függő módon jelezte azok kompetitív képességét: a torokfolt mérete pozitívan korrelált a nyerési valószínűséggel a tojóknál, de nem a hímeknél. Eredményeink azt sugallják, hogy ebben a fajban a táplálékszerzés közben kialakult összetűzések kimenetelét nem határozza az egyedek felfedező viselkedése. Eredményeink először utalnak arra, hogy a begyfolt státuszjelző tollazati jellegként működhet a tojók esetében is mezei verebeknél.

2. vizsgálat. Fülöp és mtsai. (2019) Személyiség és szociális táplálkozási taktikák használata szabadon élő mezei verebeknél (*Passer montanus*). *Behavioral Ecology* 30(4): 894–903. DOI: https://doi.org/10.1093/beheco/arz026

Szociális táplálkozás alatt az egyedek gyakran alternatív viselkedési taktikákat alkalmaznak a táplálék megszerzésére: a keresők aktívan keresik a táplálékot, míg a potyázók a keresők által talált táplálékot fogyasztják. Bár a szociális táplálkozási taktikák használata részben rugalmas, egyes egyedek hajlamosak többet keresni, míg mások nagyrészt inkább potyáznak. Ez az egyedi szintű

mintázat a taktikahasználatban nagyban hasonlít az állati személyiség jelenségére, azonban a személyiség és a szociális táplálkozási taktikák használata közötti viszony nem teljesen tisztázott. Vizsgálatunkban az egyedek felfedező viselkedése és a szociális táplálkozási taktikák használata közötti kapcsolatot teszteltük szabadon élő mezei verebeknél két téli időszak alatt. Az egyedek személyisége ivar-specifikus módon prediktálta a különböző szociális táplálkozási taktikák használatát: míg a felfedezőbb tojók többet potyáztak, a hímeknél ez a kapcsolat nem volt szignifikáns. Ivartól függetlenül, a potyázás valószínűsége nőtt az egységnyi területre vetített táplálkozó egyedek denzitásával, és a potyázás valószínűsége magasabb volt, ha a táplálékszerzés a táplálkozási esemény végén történt. Eredményeink rámutatnak, hogy az egyedi viselkedésbeli különbségek befolyásolhatják a szociális viselkedést, így hatással lehetnek a szociális evolúció folyamatára.

3. vizsgálat. Fülöp és mtsai. (2021) Egyedi személyiség ivar-specifikus tollazati jelzése egy énekesmadár fajnál. *Behavioral Ecology and Sociobiology* 75: 38. DOI: https://doi.org/10.1007/s00265-021-02971-z

Szociális környezetben úgy a hím, mint a tojó egyedek tollazati jelzéseket alkalmazhatnak az intraspecifikus kommunikáció során. A különféle tollazati jelzések szerepét első sorban a párválasztás kontextusában vizsgálták mélyrehatóan, többnyire szexuálisan dimorf fajoknál. Kevesebb figyelmet fordítottak azonban a színezeti jellegek tanulmányozására olyan fajokban, amelyeknél gyenge vagy teljes mértékben hiányzik a szexuális dimorfizmus. Az ilyen fajoknál mindkét ivar rendelkezhet ugyanazzal a tollazati jelleggel, de annak jelzőértéke a hímeknél és tojóknál akár eltérő is lehet. Vizsgálatunkban szabadon élő mezei verebek begyfoltmérete és három fenotípusos jelleg közötti kapcsolatot teszteltük, különös tekintettel az ivari különbségekre. A fenotípusos jellegek a következőek voltak: kondíció (testméretre korrigált testtömeg), fiziológiai állapot (veleszületett immunitás, amelyet az összfehérvérsejt szám által fejeztünk ki, valamint a krónikus fiziológiai stressz mértéke, amelyet a heterofilok és a leukociták arányával jellemeztünk) és az egyedi személyiség (aktivitás új környezetben). Az egyedek begyfolt mérete a hímeknél negatívan-, míg a tojóknál pozitívan korrelált az aktivitással. Továbbá, a begyfolt mérete mindkét ivar esetében pozitív összefüggést mutatott a krónikus stressz mértékével, de nem függött össze a veleszületett immunitás mértékével és a

kondícióval sem. Eredményeink arra utalnak, hogy ugyanazon tollazati jelleg ivar-specifikus jelzőértékkel bírhat, esetlegesen más szerepet ellátva hímek és tojók esetében.

4. vizsgálat. Vágási I.C.*, Fülöp A.* és mtsai. (2021) A változatos személyiség-összetételű csoportok csökkentik a fiziológiai stressz mértékét egy énekesmadár fajnál. *Proceedings of the Royal Society B: Biological Sciences* 288(1943): 20203092. DOI: https://doi.org/10.1098/rspb.2020.3092 (*megosztott első szerzők)

A csoport fenotípusos (pl. személyiség) összetétele befolyásolhatja annak működését. A csoportösszetétel ugyanakkor a csoportot alkotó egyedek állapotára és rátermettségére is hatással lehet. Ez utóbbi hatásról azonban empirikus tanulmányok eddig nem születtek, holott a csoportos életnek ez egy releváns aspektusa lehet a szociális szelekció megértése és az egyedi viselkedésbeli sokféleség evolúciós fennmaradása szempontjából. Vizsgálatunkban házi veréb (*Passer domesticus*) csoportok személyiség összetételét manipuláltuk, majd teszteltük ennek hatását az egyedek fiziológiai állapotára (kondíció, krónikus fiziológiai stressz, oxidatív stressz és veleszületett immunitás). Eredményeink azt mutatják, hogy a változatos személyiség-összetételű csoportokban az egyedek kondíciója jobb, illetve a fiziológiai stressz és az oxidatív károsodásának mértéke szignifikánsan alacsonyabb, mint a kevésbé változatos összetételű csoportokban. Vizsgálatunk azt támasztja alá, hogy a szociális környezet befolyásolja a csoporttagok fiziológiai állapotát. A csoportok fenotípusos összetételének ismerete, tehát, kulcsfontosságú lehet a szociális csoportok szerveződési szabályainak és a csoportösszetétel evolúciós következményeinek megértése érdekében.

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Part II.

This part contains the original scientific publications and manuscripts which constitute the foundation of this thesis.

List of publications

1. **Fülöp, A.**, Németh, Z., Kocsis, B., Deák-Molnár, B., Bozsoky, T., Csöppü, G., Barta, Z. (2022) Fighting ability, personality and melanin signalling in free-living Eurasian tree sparrows (*Passer montanus*). (submitted manuscript)

2. **Fülöp, A.**, Németh, Z., Kocsis, B., Deák-Molnár, B., Bozsoky, T., Barta, Z. (2019) Personality and social foraging tactic use in free-living Eurasian tree sparrows (*Passer montanus*). *Behavioral Ecology* 30(4): 894–903. DOI: https://doi.org/10.1093/beheco/arz026

3. **Fülöp, A.**, Lukács, D., Fábián, P.I., Kocsis, B., Csöppü, G., Bereczki, J., Barta, Z. (2021) Sex-specific signalling of individual personality by a mutual plumage ornament in a passerine. *Behavioral Ecology and Sociobiology* 75: 38. DOI: https://doi.org/10.1007/s00265-021-02971-z

4. Vágási, C.I.*, **Fülöp, A.***, Osváth, G., Pap, P.L., Pénzes, J., Benkő, Z., Lendvai, Á.Z., Barta, Z. (2021) Social groups with diverse personalities mitigate physiological stress in a songbird. *Proceedings of the Royal Society B: Biological Sciences* 288(1943): 20203092. DOI: https://doi.org/10.1098/rspb.2020.3092 (*shared first authorship)

Personal contribution to the studies included in the thesis

	Study 1	Study 2	Study 3	Study 4
Original idea	●	●	●	●
Study design and data collection	●	●	●	●
Data analysis	●	●	●	●
Manuscript preparation	●	●	●	●

Study 1

Fighting ability, personality and melanin signalling in free-living Eurasian tree sparrows (*Passer montanus*)

Fighting ability, personality and melanin signalling in free-living Eurasian tree sparrows (*Passer montanus*)

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Abstract

Background. Individuals' access to resources is often decided during dyadic contests the outcome of which is determined by the fighting (or competitive) ability of the participants. Individuals' fighting ability (termed also as resource-holding power or potential, RHP) is usually associated with individual features (e.g. sex, age, body size) and is also frequently signalled through various ornaments, like black throat patches (bibs) in many birds. Individual personality is a behavioural attribute often linked to fighting ability as well. Based on earlier studies, however, the relationship between personality and fighting ability is far from being straightforward. While accounting for sex and body size, we studied whether exploratory behaviour, an aspect of personality, predicts fighting ability when competing for food during winter in free-living Eurasian tree sparrows (*Passer montanus*). We also investigated whether bib can serve as a potential indicator of individual competitiveness in this species.

Methods. We have captured adult tree sparrows, marked them with a unique combination of colour rings, and collected data about the individuals' sex, body size, bib size and exploratory behaviour. Birds were then released and the agonistic behaviour of the marked individuals was recorded while foraging in groups on bird feeding platforms.

Results. The probability of winning a fight, a proxy for fighting ability of individuals, was not related to exploratory behaviour, in any of the sexes. However, bib size was positively related to probability of winning in females, but not in males. Body size was not associated with probability of winning neither in males, nor in females.

Conclusions. Our results suggest that, at least in tree sparrows, the outcome of dyadic encounters over food during the non-breeding period are not determined by the exploratory personality of individuals. However, our findings provide further support for a status signalling role of the black bib in tree sparrows, and hint for the first time that bib size might function as a status signal in females as well. Finally, our results do not confirm that body size could serve as an indicator of fighting ability (i.e. RHP) in this species.

Keywords: competition, contest, resource-holding potential, exploratory behaviour, sex

differences, badge of status, *Passer montanus*.

Introduction

Resources (e.g. food, mate, breeding territory) are typically limited in nature, hence access to them directly influences individuals' fitness (e.g. Ellis 1995, Majolo et al. 2012). In order to gain access to limited resources individuals often engage in dyadic agonistic interactions. The outcome of these contests (i.e. winning or losing) is expected to be largely determined by the relative fighting ability of individuals (resource-holding power or potential, RHP; Parker 1974, Maynard Smith and Parker 1976, Arnott and Elwood 2009).

Fighting ability was found to be associated with several individual traits. For instance, in a handful of species chances of winning a fight are higher for males than for females (e.g. Richner 1989, Briffa and Dallawaym 2007; but see Couchoux et al. 2021), or for adults than for juveniles (e.g. Richner 1989, Couchoux et al. 2021). Also, larger individuals usually more often win than smaller ones (e.g. Richner 1989, Lindström 1992, Briffa 2008, Chamorro-Florescano et al. 2011, Rudin and Briffa 2011, Couchoux et al. 2021). Besides, fighting ability was found to be related to certain individual behavioural characteristics as well, like problem solving capacity (less competitive individuals are better problem-solvers; e.g. Cole and Quinn 2012, O'Shea et al. 2017) or personality (see below).

Individual personality is commonly defined as consistent among-individual differences in behaviour across time and/or contexts (Dall et al. 2004, Realé et al. 2007) and includes traits as activity, exploration-avoidance, boldness-shyness, sociability or aggressiveness (Realé et al. 2007). Personality and fighting ability are proposed to covary due to multiple reasons. From a proximate view, personality and fighting ability can be linked by common physiological mechanisms regulating individual behaviour (e.g. metabolic rate, hormones; Briffa et al. 2015). Such a link is suggested by the differences in the individual life-history strategies and related physiological profiles of individuals with different personalities, as proposed by the "pace-of-life syndrome" (POLS) framework (Realé et al. 2010). Accordingly, individuals with a fast pace-of-life are expected to have a life-history strategy that favours reproduction at the cost of survival (i.e. live fast), a physiological profile characterized by a high metabolic rate, low hypothalamic–pituitary–adrenal (HPA) axis reactivity and low immune response, and more proactive behaviour (i.e. more active, exploratory, bold, and aggressive). In contrast, individuals with a slow pace-of-life should have a life-history that promotes survival over reproduction (i.e. live slow), a physiology marked by a low metabolic rate, high HPA axis reactivity and high immune response, and a more reactive behaviour (i.e. less active and exploratory, shy, and less aggressive) (Realé et al. 2010). It has to be noted, though, that empirical evidence for POLS is mixed (e.g. Royauté et al. 2018, Moiron et al. 2020), probably because important effects influencing trait correlations have been largely neglected in most of the studies (e.g. sex, ecological conditions; Hämäläinen et al. 2018, Immonen et al. 2018, Montiglio et al. 2018, Tarka et al. 2018, reviewed by Dammhahn et al. 2018). Nevertheless, support for POLS exists (e.g. Dhellemmes et al. 2021), but an overall refinement of the integration of life-history, physiology and personality is needed (Laskowski et al. 2021). From an ultimate perspective, personality differences can be maintained by various evolutionary mechanisms (e.g.

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differences in state, frequency-dependent selection, environmental variation or non-equilibrium dynamics; Wolf and Weissing 2010). Frequency-dependent selection, for instance, can result the adaptive coexistence of individuals with different personalities, if the fitness benefits of individuals is dependent on the frequency of other personality types in the population, similarly to the different competitive strategies, modelled as Hawk-Dove game, or to the different social foraging strategies, modelled as producer-scrounger game (Wolf and Weissing 2010). Previous studies have shown that proactive/reactive individuals often play different frequency-dependent behavioural strategies in different contexts (e.g. producer-scrounger tactics during foraging; Kurvers et al. 2010, Fülöp et al. 2019). Thus, fighting ability and individual personality are expected to be correlated, on one hand, due to the possibly linked physiological mechanisms of the two behaviours, and on the other hand, by the same evolutionary mechanism maintaining the two behaviours (Briffa et al. 2015). However, it is still not entirely clear which personality traits contribute more to the fighting ability of individuals and how they are related.

Numerous studies have investigated the relationship between fighting ability and personality in both invertebrates and vertebrates, but reported contrasting results. For instance, bolder *Actinia equina* sea anemone individuals were more likely to be winners in contests over territory (Rudin and Briffa 2012, Lane and Briffa 2017). Similarly, more exploratory great tits (*Parus major*) were also better capable of monopolizing a food source (Cole and Quinn 2012). In contrast, bolder speckled wood butterflies (*Pararge aegeriahermit*) were not more likely to win contests for sunspot territories (Keiser et al. 2019); and bolder hermit crabs (*Pagurus bernhardus*) did not have a higher attacker success rate when fighting over shells providing shelter, but less bold individuals were better defenders (Courtene-Jones and Briffa 2014). Furthermore, another study in great tits found no relationship between exploratory behaviour and food resource utilization (O'Shea et al. 2017). Overall, as suggested even by this non-exhaustive list of previous findings, the relationship between fighting ability and personality is not always straightforward and appears to be intricate.

Engagement of individuals in competitive interactions, and their outcomes, can be shaped by different intrinsic- and extrinsic factors. For instance, phenotypic (e.g. sex, age, size, personality) differences between participants (see references above) or their fighting skills (Briffa and Lane 2017) can shape contests. Motivation (Nosil 2002), resource value (Arnott and Elwood 2007), previous experience (e.g. through the "winner-loser effect"; e.g. Stuart-Fox and Johnston 2005, Condon and Lailvaux 2016; reviewed by Hsu et al. 2006, Rutte et al. 2006) or role asymmetry (e.g. prior resident vs. newly arrived individual, resource owner vs. intruder; Snell-Rood and Cristol 2005, Sacchi et al. 2009, Chamorro-Florescano et al. 2011) can also affect individuals' engagement and success in contests. Contests can also be influenced by context (e.g. social context; Verbeek et al. 1996, 1999). Since fights can be affected by this large array of factors, identification of individual determinants of fighting ability may become challenging, especially in natural populations. For instance, many social species live in fission-fusion societies, meaning that groups regularly split and reunite, on which occasions group composition and hence social context can change unpredictably. When group characteristics (e.g. size, sex ratio, phenotypic composition) change, many of the factors listed above can change as well.

To minimize the costs of among-individual conflicts, various signalling mechanisms have evolved in many species (e.g. colour traits, behavioural displays, vocalizations), through which individuals can communicate their fighting ability and/or dominance status, towards conspecifics (Maynard Smith and Harper 2003, Tibbetts 2013, Tibbets et al. 2022). One potential signal associated with status is melanin-based colouration ("badges of status"; e.g. Rohwer 1975, Järvi and Bakken 1984, Hoi and Griggio 2008, Chaine et al. 2011, Rat et al. 2015; reviewed by Santos et al. 2011). Melanins (eumelanin and pheomelanin) are pigment molecules, responsible for the grey, brown and black colouration of the integument. Since melanins are endogenously synthesized, in contrast to carotenoid pigments, which are acquired through the diet, the "honesty" of melanin-based colour signals has frequently been questioned (e.g. Jawor and Breitwisch 2003). Evidence, however, suggest that melanin-based colouration can function as honest signal of individual quality (e.g. McGraw 2008; reviewed by Guindre-Parker and Love 2014). Nevertheless, the mechanisms linking melanin-based colouration and condition can be complex (e.g. D'Alba et al. 2014). In some species, such as the Eurasian tree sparrow (*Passer montanus*), melanin-based ornaments are possessed by both sexes (i.e. "mutual ornamentation"; Kraaijeveld et al. 2007). Interestingly, mutual ornamental traits in different species can have either a similar or different signalling function in the two sexes (similar, e.g. Rohwer 1975, Järvi and Bakken 1984, Pöysä 1988, Rat et al. 2015; different, e.g. Fargallo et al. 2014, Matsui et al. 2017, Mónus et al. 2017, Fülöp et al. 2021).

The Eurasian tree sparrow is a small-sized, highly gregarious passerine which forages in large flocks (up to 80 individuals at our study site; Mónus and Barta 2010, pers. obs.) during the winter (Summers-Smith 1995, Barta et al. 2004). Although male and female tree sparrows are apparently sexually monochromatic to the naked human eye, a study found evidence for dichromatism in this species in the UV range (Eaton 2005). Sexes are similar in size, though males are slightly larger than females with a large overlap in body size measures of the two sexes (Mónus et al. 2011). Both males and females possess a black bib patch (hereafter "bib"), which is a conspicuous eumelanin-based plumage ornament. As a previous study suggests, it can have a sex-dependent status signalling role: it may indicate fighting success in males, but not in females (Mónus et al. 2017). Nevertheless, the status signalling role of the bib in females cannot be ruled out, since no other studies, beside the one by Mónus et al. (2017), investigated this question in the two sexes separately. The size of the bib in males is larger than those of females but, similarly to body size measures, there is a considerable overlap between the sexes in this aspect as well (Mónus et al. 2011, Fülöp et al. 2021). Here, we study whether an axis of individual personality, namely exploratory behaviour, predicts fighting ability in free-living Eurasian tree sparrows, in a social foraging context during the non-breeding season (i.e. wintering). We also investigate if fighting ability is communicated towards conspecifics through the individuals' black bib, in other words, whether the bib has any status signalling role. We study these relationships in the light of the individuals' sex and body size.

Materials and Methods
Study site and period
The study was carried out in the Botanical Garden and the Central Campus of the University

of Debrecen (Debrecen, Hungary) during the wintering seasons (i.e. between mid-October and mid-March) of 2013/14, 2014/15 and 2015/16. Birds were trapped, marked and tested for exploratory behaviour during all the three seasons of the study, while data on agonistic interactions were collected during the last two wintering seasons (see also Fülöp et al. 2019). The study site is an open area with scattered trees and bushes, also containing some buildings of various sizes forming a heterogeneous semi-urban landscape mosaic. Further details about the study site are given in Barta et al. (2004) and Fülöp et al. (2019).

Both the bird trapping procedures and the observations on the social behaviour of individuals were performed on three feeders installed at our study site. Feeders consisted of wooden platforms made of oriented strand board (120 × 120 cm) placed on the ground (Fülöp et al. 2019). During all three wintering seasons, we provided *ad libitum* food (sunflower seeds) for the birds on a daily basis, on all the feeders throughout the whole winter period, except periods when recordings of social behaviour were made (see below; Fülöp et al. 2019).

Field procedures

Field procedures were the same as described in Fülöp et al. (2019). We captured tree sparrows with mist nets (Ecotone, Poland; https://www.ecotone.com.pl/) at bird feeders each winter between mid-October and mid-January, except the first wintering season (2013/14), when birds were captured during the whole winter (i.e. between mid-October and mid-March). At capture, we fitted each individual with a standard ornithological metal ring, issued by the Hungarian Bird Ringing Centre, which was supplemented with a unique combination of three plastic colour rings, enabling the identification of the marked individuals from distance. Furthermore, we measured body mass (± 0.1 g with a Pesola spring balance), tarsus length (± 0.01 mm with a digital caliper) and wing length (± 0.5 mm with a ruler); and because sexes are alike in terms of appearance and size in tree sparrows (Mónus et al. 2011), we also took a blood sample (~ 50–150 µl) from the brachial vein of the birds to carry out molecular sex determination of individuals (for details, see Fülöp et al. 2019, 2021). To quantify bib size (i.e. area; mm^2), we photographed the black bib of the birds on the field and measured bib area subsequently from the photographs with the ImageJ software (ver 1.51i ran on a Linux operating system; https://imagej.nih.gov/ij/index.html). While preparing the photographs, we held the focal individual in a standardized position: the head of the bird facing the camera so that the axis of the beak being perpendicular to the axis of the body and the camera sensor plane. We also included on each photograph a standard reference for length (i.e. ruler or millimetre paper), which was necessary to calibrate unit length during measurements. Measurements were completed in three steps for every individual: first, we calibrated unit length on the photograph using the "set scale" function of ImageJ, then we traced the outline of the black bib patch with the highest accuracy possible using the "freehand selection" tool, and lastly, we obtained bib area using the "measure" function. All bib size measurements were carried out by the same person (AF). To increase measurement precision of our data, we measured bib size for each individual from the same photo twice and averaged the values. Repeatability of the two measurements was high (intraclass correlation coefficient, performed with the "ICC" package for R (Wolak et al. 2012, R Core Team 2021): ICC = 0.991, 95% CI = 0.988–0.994, N = 175). Finally, each individual was tested for exploration (see below).

After completing all the procedures, individuals were released at the site of their capture. Between 2013 and 2016, we individually marked 194 tree sparrows in total (80 males and 114 females) (Fülöp et al. 2019).

Quantifying exploratory behaviour

We measured exploratory behaviour of individuals using the standard open-field test (Dingemanse et al. 2002). The tests and further statistical analyses of the data were carried out as detailed in Fülöp et al. (2019). Briefly, we recorded the behaviour of each individual for 10 min in a novel environment (i.e. an empty room with four artificial trees; room size: 3.25 × 2.55 × 1.95 m (L × W × H)) using a handheld video camera (Panasonic HC-V510) through a one-way mirror window. Recordings were made by one the two observers (AF or ZN). Then, from each video, we coded a series of events, as follows: the time of the first landing of the focal individual after its release into the test room, the time of its first movement after the first landing, the number and type of movements performed, and its propensity to explore the test room. We distinguished 3 different movement types: hops (short distance movements performed either on the ground or on the trees without the bird using its wings), flight-assisted hops (short distance movements combining hops that are assisted with usually 1 wing beat), and continuous flights (longer distance movements, lasting usually a few seconds, where the bird performs typical flight). We characterized the individuals' propensity of exploration of the test room by dividing the test room into 8 equal-sized imaginary compartments and counting the number of occurrences of the focal individual in the different compartments of the room. Compartment limits of the test room were marked by reference lines painted on the walls of the room. All videos were analysed by the same person (TB) with a video analysis software ("mwrap"; Bán et al. 2017).

Using the events coded from the videos, we first calculated the variables "movement latency" (s; i.e. the time elapsed between the first landing of the individual in the test room and its first movement), cumulative "number of movements" performed during the test (i.e. sum of the three movement types), "number of different compartments visited" (i.e. ranging 1-8) and "total number of position switches between compartments" of the test room (i.e. sum of the position switches between compartments). Then, using these four variables, we performed a principal component analysis (PCA) and extracted predicted values for the first principal component (PC1). PC1 strongly correlated with three of the four behavioural variables measured, the exception being "movement latency"; and explained 65.95% variance, having the following loadings for "number of movements" during the test, "number of different compartments visited" and "total number of position switches between compartments" of the test room: 0.556, 0.534 and 0.518, respectively. Therefore, we used these predicted values from PC1 to characterize exploratory behaviour of individuals. Note that higher PC1 scores indicate a higher exploratory tendency of individuals. In total, between 2013 and 2016 we tested 189 individuals (78 males and 111 females) for exploration.

In order to confirm that exploratory behaviour is a personality trait in tree sparrows, we have tested a subset of individuals (N = 48 individuals, 20 males and 28 females) multiple times for exploration (45 individuals twice and 3 individuals three times). Exploratory behaviour was significantly repeatable (adjusted repeatability calculated with a linear mixed-

effects model with normal distribution, R package "rptR" (Stoffel et al. 2017): r = 0.455, SE = 0.105, 95% CI = 0.253–0.669, P < 0.001, P_{perm} = 0.002; see Fülöp et al. 2019 for details). For repeated individuals, we used the exploration score of their first exploration test in the subsequent statistical analyses.

Assessment of fighting ability

In order to determine individual fighting ability we recorded agonistic social interactions between sparrows while foraging socially on feeders during the last two seasons of the study (2014/15 and 2015/16) at two of the feeders (for details see Fülöp et al. 2019). During the season 2014/15, recordings were made on 17 different days, between 7 January and 11 February 2015, while during the season 2015/16, on 29 different days, between 21 January and 4 March 2016. Recording sessions were performed during daytime (between 8 AM and 5 PM; GMT +1), overlapping with the activity period of the tree sparrows during the winter. During the recording sessions, we restricted individuals' access to food to stimulate the emergence of various forms of social interactions between them (i.e. agonistic interactions and producer-scrounger foraging tactic use; Fülöp et al. 2019). To do this, we placed a second layer of oriented strand board of matching size on the feeders which contained 121 holes (diameter: 24 mm, depth: 18 mm, distance between adjacent holes: 10 cm) arranged in a 11 by 11 rectangular grid (Fig. 1). Before the start of the video recording sessions we first removed all the food from the feeder, then filled 10 randomly selected holes with one teaspoon of corn grit. During a recording session we typically recorded multiple foraging bouts. A foraging bout started when the first individual arrived at the feeder and ended when the last bird from the flock flew away from it. The recordings were made by one of three observers at a time (AF, ZN and ZB) using a video camera (Panasonic HC-V510) without disturbing birds (for details see Fülöp et al. 2019).

Fig 1. Snapshot from a video recording illustrating the feeding platforms used in the study and several Eurasian tree sparrow (*Passer montanus*) individuals, including also colour-ringed

birds, in a typical social foraging context. The feeding platform is made of two layers of oriented strand board, the upper layer containing 121 holes arranged in a 11 by 11 grid (see Methods for details).

Agonistic interactions between pairs of individuals (i.e. dyads) from the videos were analysed subsequently following Mónus et al. (2017) by the same person (GC). Agonistic interactions included various forms of behaviour exhibited by one or both of the participants, such as displacement, displaying, pecking and/or fighting. For each dyadic interaction in which at least one colour marked individual was involved, we noted the identity of the initiator, the winner and the loser. In total, we have recorded a total of N = 581 fights, out of which N = 74 were fights where no clear winner and loser could be recognized. These latter fights were excluded from the statistical analysis. Also, since no exploration data was available for 2 marked individuals, another N = 16 fights were discarded from the data. Our final data set thus set contains N = 491 agonistic interactions with an unambiguous outcome from 32 different individuals, of which 14 were males and 18 were females (mean number of fights per individual = 17.09, SD = 22.48, median = 7.00, range = 1–106).

We characterised the fighting ability of individuals using the probability of winning as an index. Instead of calculating dominance rank for individuals, we used winning probability because for the majority of fights (N = 445, 87.77% of the total fights) the identity of only one participant is known and calculating dominance ranks using a data set with a similar structure is not possible (Sánchez-Tójar et al. 2018a). However, fighting ability (i.e. RHP) is an important individual attribute determining dominance status (Tibbets et al. 2022), and indeed many previous studies (e.g. Liker and Barta 2001, Dingemanse and de Goede 2004, Cole and Quinn 2012) have shown that fighting ability of individuals is correlated with their dominance status.

Statistical analyses

All calculations and statistical analyses were performed in the R statistical environment version 4.1.2 (R Core Team 2021) run in R Studio version 2021.9.0.351 (RStudio Team 2021). We have analysed the relationship between individual phenotypic traits and fighting ability with a Bayesian generalized linear mixed-effects model with a binomial response distribution and logit link function, as implemented in the R package "brms" (Bürkner 2017), an interface for Stan (Stan Development Team 2015a, b). The model contained fight outcome as a dependent variable (coded with a binary value, 0 or 1, depending whether the individual lost or won the given fight, respectively), season (2014/15 and 2015/16) and sex (male or female) as a categorical predictors, and the following continuous predictors: body size, exploration score and bib size. Agonistic behaviour of individuals, and hence chances of winning fights, can show strong temporal variations on different time scales, as follows. Since tree sparrows usually arrive sequentially on the feeder within a foraging bout, competition between individuals can change (presumably increase) with the time spent on the feeder. Hence, the probability of winning can change within a foraging bout. Furthermore, behaviour of individuals can vary also during the day, due to the daily variation in individuals' energy reserves, and can also change over the season, owing to changes in environmental conditions

(e.g. temperature). Therefore, to control for these possible effects, we entered into the model the time of the agonistic event within the foraging bout (expressed in seconds passed from the start of the foraging bout), and the date (expressed as Julian date, day 1 = 1st January) and time of the foraging bout (expressed as minutes spent from midnight), as continuous predictors. In addition to the above listed main effects (i.e. categorical and continuous effects), we have tested in the model all the second order interactions of season and sex, with the continuous predictors. Individual ID and foraging bout ID were entered in the model as two crossed random effects, to control for repeated measurements from the same individuals and potential temporal autocorrelation in behaviour within the same foraging bout, respectively. Although we carried out our observations on two different feeders, we did not include this effect in our final analysis, since entering feeder ID as a categorical predictor and its' interactions with the continuous variables in the model resulted in convergence difficulties in a preliminary phase of the analysis, due to the moderate sample sizes in terms of number of individuals (N = 32 individuals), and due to the uneven distribution of sexes across seasons and feeders, respectively. For the same reason we omitted also the interaction between season and sex from the model. Nevertheless, *a priori* we are not expecting a strong effect of feeder location on the relationship between individual traits and fighting success, since the two feeders were located close to each other (aprox. 400 m) in the same habitat. Body size was expressed using predicted values of the first principal component (PC1) extracted from a PCA ("prcomp" function in R, package "ade4"; Dray and Dufour 2007) that included body mass, tarsus length and wing length of individuals, all measured at capture (see above). Only PC1, which explained 62.97% of the total variation, had an eigenvalue >1 and it had the following loadings for body mass, tarsus length and wing length, respectively: 0.639, 0.572 and 0.514. Prior to entering into the model, bib size values and time of the agonistic event within the foraging bout were log-transformed to handle the skewness of these variables, and all the continuous predictors were Z-transformed (mean = 0, SD = 1) using the "scale" function in R to facilitate model convergence. We ran the model with default priors (i.e. relatively uninformative priors), 4 Hamiltonian Monte Carlo chains, each chain for 12000 iterations, and using a warm-up period of 2000 iterations. We checked model convergence using trace plots and Rhat values (all Rhat = 1). *Post-hoc* comparisons between different slopes of continuous predictors involved in interactions with a 95% credible interval not overlapping 0 (i.e. effects considered "significant" in a frequentist sense) were performed using the R package "emmeans" (function "emtrends" in R; Lenth 2020). Plots were made using the R package "ggplot 2" (function "ggplot" in R; Wickham 2016).We report posterior means for all estimated parameter coefficients ± 95% credibility intervals (CrI) or 95% highest posterior density intervals (HPDI).

Ethical note

Tree sparrows were ringed under a license from the Hungarian Bird Ringing Center (license nr. 390 accredited to ZB) and permission for the study was granted by the Hajdú-Bihar County Governmental Office, District Office of Debrecen - Department of Environmental and Nature Protection (permit nr. HB/10-KTF/00487-1/2016). The study complies with the European laws regarding animal welfare, and adheres to the ASAB/ABS guidelines for the

use of animals in behavioural research.

Results

Among the individual traits, exploratory behaviour and body size were not related to the probability of winning a fight either alone or in interaction with sex (all 95% CrI overlap 0; Table 1). However, winning probability and bib size were associated in a sex-dependent manner (Table 1; Fig. 2); and *post-hoc* comparisons revealed that females with larger bibs were more likely to win a fight ($\beta = 3.16$, 95% HPDI = 0.75–6.37), whereas in males bib size did not predicted fight outcome ($\beta = -1.41$, 95% HPDI = -4.08–0.91).
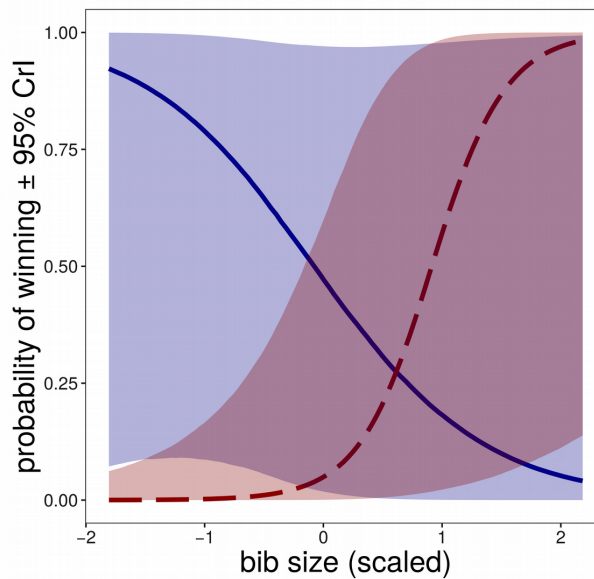
Fig 2. Sex-dependent relationship between bib size and probability of winning in free-living Eurasian tree sparrows (*Passer montanus*). Values represent model predicted conditional effects when all other predictors are held constant apart from the plotted interaction. Lines and shaded areas are model predicted logistic regression lines ± 95% credible intervals (CrI). The blue solid line indicates males, while the red dashed line indicates females.

Probability of winning a fight showed no marked temporal variations at any of the temporal scales considered. Probability of winning was not associated with the time of the agonistic event within the foraging bout in any of the sexes (Table 1). Similarly, neither date nor time of the foraging bout were associated with probability of winning, in males or females (Table 1). Finally, probability of winning was similar in the two seasons of the study, and the relational patterns between probability of winning and the continuous predictors we have tested were similar in the two seasons of the study (all 95% CrI of the interactions between season and the continuous predictors included 0; Table 1), indicating no strong annual variations in the studied associations.

Table 1. Summary of the Bayesian generalized linear mixed-effects model containing the parameter estimates of the predictors of fighting ability (i.e. probability of winning). Reference levels for the categorical variables "Season" and "Sex", are 2014/15 and males, respectively. Therefore, the reported estimates show the extent to which season 2015/16 and females differ from season 2014/15 and males, respectively. The sign of estimates indicates the direction of associations. Effects for which the 95% credible interval (CrI) does not overlap zero (i.e. considered "significant" in a frequentist sense) are highlighted in bold. R^2 for the Bayesian regression model is 0.41.

Group-level effects:

	Estimate	Est.Error	l-95% CrI	u-95% CrI	Rhat	Bulk_ESS	Tail_ESS
sd (Foraging bout ID)	**1.53**	**0.38**	**0.82**	**2.33**	**1**	**7458**	**11143**
sd (Individual ID)	**2.70**	**0.85**	**1.46**	**4.73**	**1**	**11983**	**17554**

Population-level effects:

	Estimate	Est.Error	l-95% CrI	u-95% CrI	Rhat	Bulk_ESS	Tail_ESS
Intercept	-0.11	1.91	-3.98	3.54	1	19168	22568
Season (2015/16)	-1.24	1.62	-4.39	1.97	1	20117	22718
Sex (female)	-2.96	1.93	-7.18	0.47	1	16221	18978
Body size	1.00	1.87	-2.61	4.82	1	12888	17526
Bib size	-1.46	1.51	-4.60	1.38	1	14008	18547
Exploration	-1.13	1.70	-4.77	1.98	1	14431	14771
Date	0.85	0.79	-0.66	2.45	1	19923	23041
Time	-0.20	0.65	-1.50	1.07	1	24029	27025
Time within foraging bout	0.45	0.55	-0.62	1.52	1	23975	27241
Season (2015/16):Body size	0.77	1.10	-1.46	2.90	1	18778	23458
Season (2015/16):Bib area	-0.02	0.99	-2.00	1.93	1	23269	26327
Season (2015/16):Exploration	1.03	1.47	-1.66	4.19	1	16872	17003
Season (2015/16):Date	-0.52	0.82	-2.19	1.05	1	19520	24326
Season (2015/16):Time	0.19	0.66	-1.10	1.49	1	25423	26612
Season (2015/16):Time within foraging bout	-0.24	0.53	-1.29	0.81	1	26256	27920
Sex (female):Body size	-2.51	2.02	-6.80	1.23	1	16069	18389
Sex (female):Bib size	**4.80**	**1.99**	**1.48**	**9.35**	**1**	**16469**	**17441**
Sex (female):Exploration	1.83	1.53	-0.85	5.22	1	14554	15657
Sex (female):Date	-0.63	0.54	-1.72	0.43	1	30635	31272
Sex (female):Time	0.21	0.36	-0.48	0.92	1	35350	31499
Sex (female):Time within foraging bout	0.06	0.36	-0.63	0.76	1	40812	32942

Discussion

In this study we investigated the relationship between fighting ability (i.e. probability of winning a fight) and an axis of individual personality (i.e. exploratory behaviour) in free-living tree sparrows during the non-breeding period (i.e. wintering) in a social foraging context. We also studied the role of the black bib, an eumelanin-based plumage ornament mutually present in both sexes in this species, as a trait potentially signalling fighting ability. After accounting for the effects of sex and body size, we found that probability of winning was not related to exploratory behaviour in any of the sexes. Bib size, however, was positively associated with probability of winning in females, but not in males. Both relationships were independent of body size, in both sexes, since body size was not associated with probability of winning, neither in males, nor in females.

Exploratory behaviour and fighting ability

Some of the previous studies concluded that individual personality traits and fighting ability might be related to each other (e.g. Cole and Quinn 2012, Rudin and Briffa 2012, Lane and Briffa 2017), while a handful of others found no support for similar relationships (e.g. Courtene-Jones and Briffa 2014, O'Shea et al. 2017, Keiser et al. 2019). Our results are in line with the latter ones, as we found no association between probability of winning a fight and exploratory behaviour in any of the sexes. This could occur, for instance, if the relationship is context-dependent. Findings supporting context-dependency of this relationship are available from great tits. For example, Verbeek et al. (1996, 1999) found that the sign of relationship between exploratory behaviour and fighting ability has changed (i.e. positive vs. negative) depending on the social context (i.e. individuals tested in small vs. large groups). Similarly, Dingemanse and de Goede (2004) found that the sign of relationship between exploratory behaviour and dominance, which was positively correlated with the proportion of fights an individual won, varied from positive to negative, depending on the territorial context (i.e. territory holding adult vs. non-territorial juvenile individuals). In tree sparrows social context, determined especially by groups' phenotypic composition, might be the most relevant one influencing trait correlations during the winter. In our study system, group composition seems to be variable both in the short term (i.e. within-season) and in the long-term (i.e. between years). In the short term, group composition can vary because tree sparrow flocks likely exhibit a fission-fusion type of group dynamics (pers. obs.). In the long term (i.e. between years), flock membership can change due to emigration/immigration and naturally occurring mortality. In both cases flocks' composition might change, potentially reshaping dominance structure of groups and/or determinants of status. Since our study was carried out on free-living individuals, part of them unmarked, we cannot rule out potential confounding effects originating from group dynamics that could influence our results.

A further explanation for not detecting an association between exploratory behaviour and fighting success may be that the relationship between the two is shaped by a variable we did not measure. Individuals included in the present study can form a mixed sample regarding factors outside the scope of this study, for instance, age, which cannot be determined on the basis of plumage characteristics or other physical traits in tree sparrows. If any such unmeasured trait is important in determining the relationship between exploratory behaviour

and fighting ability (see e.g. Dingemanse and de Goede 2004, Couchoux et al. 2021), an association between the two could remain masked. Overall, the fact that we have not found a significant relationship between fighting ability and exploratory behaviour does not exclude that a correlation still exists between the two under certain scenarios. In order to clarify these aspects, further studies are needed.

Sex-specific melanin signalling of fighting ability

The role of conspicuous melanin-based ornaments serving as badges of status has been the focus of multiple studies (reviewed by Senar 2006, Santos et al. 2011), and apparently, the signalling function of various badges of status is far more complex than it was initially expected. This phenomenon is well exemplified by the case of the house sparrow (*Passer domesticus*), where the black bib of males was considered one of the classic examples of status signalling, but the signalling role of the badge has been recently questioned by a meta-analysis (Sánchez-Tójar et al. 2018b). Our findings on a closely related, but much less studied species, the tree sparrow, are similarly intriguing. We found that probability of winning a fight was sex-dependently associated with bib size. Moreover, while in a previous study in the same population, performed 15 years earlier (i.e. winter of 1999/2000), Mónus et al. (2017) found that bib size was related to the proportion of fights won in males, but not females, here, we found that bib size was associated with a higher probability of winning a fight in females, but not in males. Our results suggest, for the first time, that bib size might have a status signalling function also in females in this species.

The opposite pattern we found regarding the status signalling function of the bib, compared to Mónus et al. (2017; see also Torda et al. 2004), might be the consequence of the marked changes in environmental factors occurring between the times of the two studies through their effect on group dynamics (e.g. size, composition). While winters at our study site in the recent years became milder with only a few days of snow coverage in each season, during the period of Mónus et al.'s (2017) study winters were considerably colder with longer periods of complete snow coverage (mean winter temperature, between mid-October and mid-March, in 1999/2000: 1.95 °C, in 2014/15: 4.35 °C, and in 2015/16: 4.36 °C; source of data: https://www.ncei.noaa.gov/access/past-weather/debrecen). Environmental conditions are capable to influence social dynamics for free-living individuals, for instance, through food availability (e.g. quantity, distribution), which can have social implications in the short-term (i.e. within-season) by influencing fission-fusion group dynamics (see e.g. del Mar Delgado et al. 2021). In the long-term (i.e. between years), environmental changes can potentially shape population structure (e.g. sex ratio, age structure, size), for instance, through regulating annual survival (e.g. Santisteban et al. 2012, Gullett et al. 2014). The contrasting results we found with Mónus et al. (2017), therefore, might be caused by population differences occurring on long-term, possibly due to environmental effects.

Similarly to exploratory behaviour, another potential explanation for the differences between the two studies can be that one or more confounding effect(s) acting on the association between bib size and fighting success which could differ between the two studies were not quantified. For instance, body condition, immunity and stress level, or parasite load are among some factors which can be listed as potential candidates. These effects have been

shown to be associated with melanin-based colouration (e.g. Fitze and Richner 2002, Wiebe and Vitousek 2015, Fülöp et al. 2021; reviewed by San-Jose and Roulin 2018). Although bib size of individuals is acquired during the autumn (i.e. between July and October), when tree sparrows perform their complete annual moult, these factors can still influence the relationship between bib size and fighting success later in winter, for instance, if bib size is an indicator of individual quality.

Finally, an additional aspect to consider, which is applicable for both studies (Mónus et al.'s 2017 study and this study), and which can influence the association between fighting ability and plumage traits both in the short-term (i.e. within-season) and in the long-term (i.e. between years), is familiarity between individuals. Familiarity can be an important factor influencing the information value of plumage signals (Chaine et al. 2018). Thus, changes in social environment, can shape the correlation between fighting ability and bib size. We need to point out that for a large fraction of the fights only one of the interacting individuals' identity is known in both studies (see Methods here and in Mónus et al. 2017). Hence, limited information is available about the familiarity between opponents in both studies.

Nevertheless, it remains an interesting question what mechanism can explain the apparent sex-specific differences in the signalling role of this mutual ornament, as found in multiple instances in tree sparrows (e.g. Matsui et al. 2017, Mónus et al. 2017, Fülöp et al. 2021, this study), and what are the ultimate consequences of it. Overall, the causes and implications of this phenomenon are poorly understood, and hence, the sex-specific signalling function of mutual colour traits needs to be further investigated.

Is body size an indicator of fighting ability?
According to theoretical studies (Parker 1974, Maynard Smith and Parker 1976), which are supported also by a large body of empirical evidence (e.g. Richner 1989, Lindström 1992, Briffa 2008, Chamorro-Florescano et al. 2011, Rudin and Briffa 2011, Couchoux et al. 2021), larger body size confers a higher RHP to individuals. Therefore, in our analysis we have accounted for the effect of body size, being a potential confounding factor in determining fighting ability of individuals. In contrast with previous expectations, however, body size was not related to the probability of winning a fight in tree sparrows, in any of the sexes.

Interestingly, our results differ again from those of Mónus et al. (2017). They found that a sex-specific relationship exists between measures of body size (i.e. body weight and wing length) and proportion of fights won. Specifically, Mónus et al. (2017) showed that in males smaller individuals, while in females larger individuals won more fights. This apparent difference between the two studies might be also the consequence of the marked changes in environmental factors occurring between the times of the two studies and its effect on social dynamics (see above). Similar dynamics occurring in the social environment of individuals might ultimately influence correlational patterns between morphological traits, like body size, and fighting ability, similarly to bib size.

Conclusions
Our study contributes to the growing knowledge on the relationship between fighting ability and individual personality. As we found no relationship between exploratory behaviour and

probability of winning, our results suggest that in tree sparrows fighting ability of individuals is independent of this personality trait. We found that bib size indicates fighting ability in females, but not in males. Although our results are contrasting with a previous study on the same species on the status signalling function of the black bib (Mónus et al. 2017), this finding provides further support for a status signalling role of bib size in this species, and for the first time in females. Finally, we found no relationship between fighting ability and body size – an individual physical traits often associated with competitiveness – in any of the two sexes. Therefore, our results do not support body size as being an indicator of RHP in this species during these years. Overall, taking also into account the correlative approach we used to investigate the above presented relationships, these thought-provoking findings emphasize the need for further, experimental studies to be carried out in controlled (social) contexts.

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Electronic supplementary material

Data to reproduce the statistical analyses will be provided as supplementary material upon acceptance.

Data accessibility

Data on the exploratory behaviour of individuals was published as part of a previous study by Fülöp et al. (2019). Data from the current study will be available as supplementary material

upon acceptance.

Author contributions
AF and ZB conceived and designed the study. AF, ZN, BK, BDM, TB, GC and ZB collected the data. AF and ZB analysed the data. AF wrote the first draft of the manuscript with significant input from ZN and ZB. All authors contributed critically to further revisions of the drafts and gave final approval for publication.

Conflict of interest
We declare no conflict of interest.

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Study 2

Personality and social foraging tactic use in free-living Eurasian tree sparrows (*Passer montanus*)

Original Article

Personality and social foraging tactic use in free-living Eurasian tree sparrows (*Passer montanus*)

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Group-foraging individuals often use alternative behavioral tactics to acquire food: some individuals, the producers, actively search for food, whereas others, the scroungers, look for opportunities to exploit the finders' discoveries. Although the use of social foraging tactics is partly flexible, yet some individuals tend to produce more, whereas others largely prefer to scrounge. This between-individual variation in tactic use closely resembles the phenomenon of animal personality; however, the connection between personality and social foraging tactic use has rarely been investigated in wild animals. Here, we studied this relationship in free-living Eurasian tree sparrows (*Passer montanus*) during 2 winters. We found that in females, but not in males, social foraging tactic use was predicted by personality: more exploratory (i.e., more active in a novel environment) females scrounged more. Regardless of sex, the probability of scrounging increased with the density of individuals foraging on feeders and the time of feeding within a foraging bout, that is, the later the individual foraged within a foraging bout the higher the probability of scrounging was. Our results demonstrate that consistent individual behavioral differences are linked, in a sex-dependent manner, to group-level processes in the context of social foraging in free-living tree sparrows, suggesting that individual behavioral traits have implications for social evolution.

Key words: exploration, open-field test, producer, scrounger, social behavior.

INTRODUCTION

A growing body of evidence from a wide range of animal taxa supports that individuals within a population show consistent (i.e., repeatable) differences over time and across contexts in their behavior; a phenomenon called animal "personality" (or "coping style," "temperament"; Koolhaas et al. 1999; Dall et al. 2004; Réale et al. 2007; Wolf and Weissing 2012). As such, individuals can be placed along a reactive-proactive continuum on the basis of correlated personality traits exhibited in response to novelty and/or conspecifics, where proactive individuals are considered to be more active, exploratory, bold, and aggressive, whereas reactive individuals are thought to be less active, exploratory, and aggressive, but more shy (e.g., Groothuis and Carere 2005; Carere et al. 2010). Furthermore, proactive individuals are characterized by lower level of behavioral flexibility, fast reaction time, and a propensity to make decisions based on superficial sampling of the environment. Reactive individuals, on the other hand, exhibit a higher level of behavioral

flexibility but with a longer response time, and they tend to make more accurate decisions based on more detailed environmental information (Koolhaas et al. 1999; Coppens et al. 2010).

Personality variations between individuals can have major ecological and evolutionary implications, as described in several organisms, through influencing key biological processes (Wolf and Weissing 2012). For instance, personality can affect life-history and/or demography by being linked to individual reproductive success (Both et al. 2005; Réale et al. 2009; Wilson et al. 2010) or survival (Dingemanse et al. 2004; Boon et al. 2008; Réale et al. 2009; Niemelä et al. 2015). Moreover, personality has been shown to be associated with dispersal capacity (Fraser et al. 2001; Dingemanse et al. 2003; reviewed by Cote et al. 2010) and/or distribution within/between habitats (Duckworth and Badyaev 2007; Sih et al. 2018), as well as with dynamics of host-parasite interactions (Dunn et al. 2011; Seaman and Briffa 2015; Horváth et al. 2016; Keiser et al. 2016). Finally, personality has been linked to various aspects of sociality as well, likely influencing social evolution. For example, personality was found to be related to social dominance (Dingemanse and de Goede 2004; Colléter and Brown 2011), leadership (Harcourt et al. 2009; Kurvers et al. 2009; Nakayama et al.

2016; Jolles et al. 2017; Sasaki et al. 2018), position of individuals within social networks (Pike et al. 2008; Croft et al. 2009; Aplin et al. 2013; Moyers et al. 2018; Sih et al. 2018), and to various aspects of social foraging (Michelena et al. 2008; Kurvers et al. 2010; Aplin et al. 2014; Keiser and Pruitt 2014; Jolles et al. 2017).

While foraging in groups, individuals usually use alternative behavioral tactics to meet their food-intake needs: some individuals, called "producers," actively search for food, whereas others, the "scroungers," look for food finders to exploit their finds (i.e., "producer-scrounger game"; Barnard and Sibly 1981; Vickery et al. 1991; Giraldeau and Dubois 2008). Although various forms of food scrounging (e.g., joining, kleptoparasitism, and pilferage) have been reported from several species, including both invertebrates (Pruitt and Riechert 2009; Dumke et al. 2016) and vertebrates (Hansen 1986; Daly et al. 1992; Hamilton and Dill 2003; Morand-Ferron et al. 2007; King et al. 2009), most of our knowledge on producer-scrounger game comes from studies carried out on avian model systems (see below). The use of producer-scrounger tactics during social foraging is modulated by several individual features, for example, sex (Aplin and Morand-Ferron 2017; but see Liker and Barta 2002), dominance status (Liker and Barta 2002; Lendvai et al. 2006; McCormack et al. 2007; Jolles et al. 2013; Keynan et al. 2015; but see Beauchamp 2006), or personality type (Kurvers et al. 2010; David et al. 2011; Jolles et al. 2013; but see Aplin and Morand-Ferron 2017). Group attributes such as size (Coolen 2002; Keynan et al. 2015; Aplin and Morand-Ferron 2017), compactness (Flynn and Giraldeau 2001; Mónus and Barta 2008), or composition (Tóth et al. 2009; Morand-Ferron et al. 2011) can further influence tactic use. Ecological factors such as predation (Barta et al. 2004; Mónus and Barta 2008) can also have an effect. The use of producer-scrounger tactics is usually flexible and frequency-dependent (Giraldeau et al. 1994; Mottley and Giraldeau 2000; Morand-Ferron et al. 2007), yet individuals usually show a preference to use one or the other tactic more frequently (e.g., Beauchamp 2001; Aplin and Morand-Ferron 2017). This consistency might mirror animal personality and hence the question naturally arises: is there any relationship between personality trait(s) and social foraging tactic use?

Interestingly, although both personality and social foraging tactic use have received increased attention from researchers in the last decades, their relationship has been covered to a lesser extent. Furthermore, studies reported contrasting results. In captive barnacle geese (*Branta leucopsis*), shy individuals scrounged more than bold ones (Kurvers et al. 2010). Exploratory behavior was not linked to scrounging, and more exploratory individuals were less successful in the role of producers in captive zebra finches (*Taenopygia guttata*; David et al. 2011). In captive rooks (*Corvus frugilegus*), bold individuals scrounged more than shy ones (Jolles et al. 2013), and finally, in wild great tits (*Parus major*), social foraging tactic use and exploratory behavior were not related (Aplin and Morand-Ferron 2017). Altogether, it seems that there is no clear pattern describing the relationship between personality and social foraging tactic use. This question is relevant, since if personality is a predictor of social foraging tactic use in animal groups, assortative grouping based on personality might determine fitness consequences for individuals through the pay-offs gained during social foraging.

We studied the connection between personality and social foraging tactic use in free-living Eurasian tree sparrows (*Passer montanus*) at bird feeders during 2 winters. Tree sparrows are small-sized passerines that forage socially on the ground, and individuals use alternative foraging tactics (i.e., producing or scrounging; e.g., Barta

et al. 2004; Mónus and Barta 2008). Based on previous studies, we formulated 2 distinct but equally plausible predictions regarding the direction of the relationship between personality and social foraging. On the one hand, proactive individuals are thought to be more superficial and anticipate fast pay-off for their actions, whereas reactive individuals are more thorough in gathering environmental information and less motivated to obtain a fast reward (Koolhaas et al. 1999; Coppens et al. 2010). Therefore, since scrounging is often associated with more imminent, predictable, and less-variable foraging success and producing is thought to be a more time-consuming activity with a potentially delayed reward (Caraco and Giraldeau 1991; Barta and Giraldeau 2000; Wu and Giraldeau 2005; but see David and Giraldeau 2011), we might predict that more explorative individuals scrounge more than reactive ones. On the other hand, proactive individuals have been shown to take more risk (van Oers et al. 2004; Cole and Quinn 2014). As producing is considered a risk prone tactic (Caraco and Giraldeau 1991; Barta and Giraldeau 2000; Wu and Giraldeau 2005), we may expect more explorative individuals to produce more than less explorative ones.

MATERIALS AND METHODS

Study site and period

The study was conducted in the Botanical Garden (hereafter "Garden") and Central Campus (hereafter "Campus") of the University of Debrecen (Debrecen, Hungary). The study site is mainly an open area with scattered trees and shrubs, also containing some buildings of various sizes forming a heterogeneous semiurban landscape mosaic (Figure 1). Further details about the Garden area are provided in Barta et al. (2004). The study was performed during the wintering seasons (i.e., between mid-October and mid-March) of 2013/14, 2014/15, and 2015/16. Tree
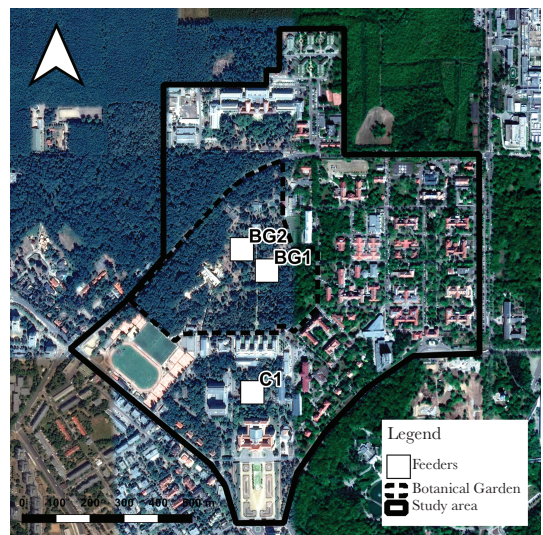

Figure 1
Map of the study area including the Central Campus (C) and the Botanical Garden (BG) areas, and the feeders used in the study. Note that the size of the symbols indicating the feeders is not proportional to the scale of the map. Background satellite image source: Google Inc.

sparrows were captured, marked, and tested for personality during all three wintering seasons, whereas data on social foraging were collected during only the last 2 wintering seasons.

Feeder setup

During the winters of 2013/14 and 2014/15, 2 feeding platforms (i.e., feeders) were installed in the Garden (feeders BG1 and BG2; Figure 1), and in the winter of 2015/16, a third feeding platform was set up in the Campus (feeder C1; Figure 1). Feeders consisted of wooden platforms made of oriented strand board (120 × 120 cm; see Supplementary Figure S1) placed directly on the ground. During all 3 seasons, we provided ad libitum food on a daily basis, consisting of sunflower seeds, on all the feeders throughout the whole winter period, except when social foraging was recorded (see below).

Field procedures

Tree sparrows were captured with mist nets (Ecotone, Poland) at the 2 feeders in the Garden, during the entire winter in the first season (2013/14), and between mid-October and end of December during the winters of 2014/15 and 2015/16. Between 2013 and 2016, we individually marked 194 adult tree sparrows in total (80 males and 114 females). Upon capture, we marked all birds with a uniquely numbered aluminum ring and with a unique combination of 3 plastic color rings. We measured body mass (±0.1 g with a Pesola spring balance), tarsus length (±0.01 mm with a digital caliper), and wing length (±0.5 mm with a ruler). We also took a blood sample (~50–150 μL) from the brachial vein of each individual to determine the sex using molecular methods (Mónus et al. 2011). The area of the black bib patch in male tree sparrows indicates dominance status in over both males and females, whereas in females, the area of the black bib patch apparently has no such signaling value (Mónus et al. 2017). However, since the signaling function of the black bib patch was studied only by correlative means in tree sparrows (Torda et al. 2004; Mónus et al. 2017), we cannot exclude a possible signaling role of the bib patch in females neither (Mónus et al. 2017). Therefore, we adopted a conservative approach and used the area of the black bib patch as a proxy for dominance status in both sexes. We photographed the black bib patch of the birds with a digital camera near a standard reference for length (i.e., ruler or millimeter paper) while holding the bird and the camera in a standardized position: birds were held on their back with their head facing the camera above so that the axis of the beak was perpendicular to the axis of the body and the camera sensor plane. Bib patch area (mm^2) was measured from digital photographs with the ImageJ software for Linux (ver 1.51i; https://imagej.nih.gov/ij/index.html), using the "set scale" function and the "freehand selection tool," by tracing the outline of the black bib patch. The ruler or the millimeter paper was used as a reference for unit length (Vágási et al. 2010). Bib patch area for each individual was measured from the same photo twice and the values were averaged to increase measurement precision in our data. Repeatability between these 2 measurements was high [linear mixed-effect model with Gaussian distribution, where bib patch area was used as a dependent variable and individual ID as a random factor, performed with the "rptR" package for R (Stoffel et al. 2017; R Core Team 2018: $r = 0.981$, SE = 0.007, 95% CI = 0.963–0.990, $P < 0.001$). Bib patch areas were measured by the same person (A.F.).

Captured birds were also subjected to a personality test, to measure their exploration (Dingemanse et al. 2002). During the 3

seasons, we used the same personality assay embedded in 2 slightly different testing protocols. We used protocol 1 during the winters 2013/14 and 2014/2015, and protocol 2 during the winters 2014/15 and 2015/16. We modified protocol 1 to increase the effectiveness of our field procedures, since protocol 1 was more time-consuming than protocol 2. Protocol 1 was implemented as follows. After capture, birds were temporarily housed in small groups (depending on the number of birds captured at a time) in an outdoor aviary [3.65 × 3.35 × 2.75 (L × W × H) m]. After a minimum of a 3-day acclimatization period, individuals were captured from the aviary in random order and tested for exploration. After completing the exploration test, individuals were released at the site of their capture. Since tree sparrows are relatively hard to recapture, in order to test the behavioral consistency of individuals, 37 individuals (17 males and 20 females) were kept in captivity for a longer period (maximum 18 days) and the exploration test was repeated. These birds were released after their second test. In total, 72 individuals (31 males and 41 females) were tested using protocol 1. In protocol 2, upon capture, birds were immediately tested for exploration without housing them in the aviary. Here, birds were ringed and sampled (for blood), and then the exploration test was carried out. Following the exploration test, measurements (including bib patch photo) were completed and the birds were released at the site of their capture. In total, 124 individuals (49 males and 75 females) were tested using protocol 2. Seven individuals (2 males and 5 females) were tested using both protocols. Within both protocols, after capture, either from the aviary or on field, birds were kept in bird bags until the exploration test was performed. Methodological discrepancies between the 2 protocols (e.g., time of blood sampling) might influence exploration scores of individuals; however, our analyses on the 2 subsets of individuals (i.e., tested either with protocol 1 or 2) show that individuals had similar scores, indicating that testing protocol did not influence behavior during the exploration test (see Supplementary Table S1).

Exploration test

We tested individuals for exploration using the standard open-field test, as described by Dingemanse et al. (2002). Tests were carried out between 7:30 AM and 4 PM (GMT +1) in a 3.25 × 2.55 × 1.95 (L × W × H) m test room (i.e., a novel environment) with artificial light. The test room contained 4 identical, artificial wooden trees, arranged symmetrically, each having 4 branches (25 cm) and a height of 1.5 m. Before the test, each test subject was placed in a dark box [45 × 29 × 42 (L × W × H) cm] connected to the test room through a sliding door, where the focal individual was kept for 15 min in order to calm down. When 15 min passed, we opened the sliding door of the cage and, in the first winter, waited for the bird to enter the test room. In the second and third winters, however, we gently stimulated the focal individual to enter the test room by knocking the wall of the box. We modified our protocol to save time, because birds frequently sat in the box (i.e., not entering the test room) when they were not stimulated to leave. Details about the distribution of individuals tested for exploration with the 2 protocols and whether they were stimulated to enter the test room are presented in Supplementary Table S2. The behavior of the individual in the test room was recorded for 10 min with a hand-held video camera (Panasonic HC-V510) through a 1-way mirror by an observer (A.F. or Z.N.).

From each video, we coded the following events: time of first landing of the individual after its release into the test room, time

of its first movement after the first landing, the number and type of movements performed by the focal individual, and the propensity to explore the test room. Movements were separated into 3 types: hops (short distance movements performed either on the ground or on the trees without the bird using its wings), flight-assisted hops (short distance movements combining hops that are assisted with usually 1 wing beat), and continuous flights (longer distance movements lasting usually a few seconds where the bird performs typical flight). Propensity of exploration of the test room was characterized by dividing the test room virtually into 8 equal-sized compartments and recording the occurrences of the individual in the various compartments of the room. Compartments of the test room were indicated by reference lines painted on the walls of the room. All videos were analyzed using the "mwrap" event recorder software (Bán et al. 2017) by the same person (T.B.). From these components of the individuals' behavior, we calculated an overall exploration score (see below).

In total, between 2013 and 2016 we tested 189 individuals (78 males and 111 females) for exploration. Out of 189, 48 individuals (20 males and 28 females) were tested more than once (45 individuals twice and 3 individuals three times) in order to calculate the repeatability of exploration. Although ringed, 5 individuals were not tested for exploration due to logistical reasons.

Social foraging

We recorded social foraging behavior of tree sparrows at 2 different feeding platforms in the second part of 2 wintering seasons (2014/15 and 2015/16). In the first season (2014/15) recordings were made only in the Garden (feeder BG2; Figure 1), whereas in the second season (2015/16) recordings were made both in the Garden (at the same feeder as in the previous year), and on Campus (feeder C1; Figure 1). During season 2014/15, recordings were carried out between 7 January and 11 February 2015 (on 17 different days), whereas during season 2015/16, between 21 January and 4 March 2016 (on 29 different days). Recording sessions were performed always between 8 AM and 5 PM (GMT +1), during the main daytime activity period of the sparrows in this period of the winter.

In both seasons, to simulate the patchy distribution of food and to force birds to search for seeds, we placed a wooden sheet on the existing feeding platforms, before the start of the video recording sessions (Barta et al. 2004). This top sheet was the same size and made of the same material as the feeding platforms (i.e., 120 × 120 cm) but contained 121 holes (diameter: 24 mm, depth: 18 mm) arranged in an 11 by 11 grid, the distance between the center of neighboring holes being 10 cm (Supplementary Figure S1; Barta et al. 2004).

Social foraging of the tree sparrows on the feeding platforms was recorded during multiple video-recording sessions. Recordings were always carried out at 1 focal feeder at a time. At the time of the recordings, birds were already accustomed to the platforms and regularly fed on them in small groups (range: 1 to 80 individuals; Mónus and Barta 2010, personal observation). Before the start of each recording session, we removed all the food from the focal feeding platform and then filled 10 randomly selected holes with 1 teaspoon of corn grit. Changing the food and/or feeder setup might influence foraging behavior of individuals in a personality-dependent way (e.g., due to neophobia); nevertheless, we found no differences in the exploration scores of individuals either observed ($\mathcal{N} = 37$) or not ($\mathcal{N} = 152$) on our feeders during the recordings of social foraging behavior (Wilcoxon rank sum test, W = 2954,

$P = 0.635$) and the exploration scores of individuals recorded on the feeders were not related to the number of times an individual was observed foraging (Spearman's rank correlation test: $r = -0.081$, $\mathcal{N} = 37$, $P = 0.635$); both results indicate that individuals with different personalities reacted similarly to changes occurring at feeders.

Tree sparrows typically stay in the bushes near the feeding platforms and forage in short bouts on the platforms (Barta et al. 2004; Mónus and Barta 2011). A foraging bout started when a bird arrived on the empty platform and ended when the last bird left the platform. Typically a group arrived over a period of time on the feeder, but foraging bouts usually ended by the sudden departure of the whole group (Barta et al. 2004; Mónus and Barta 2011). During a recording session, we filmed several foraging bouts. Filming of a bout started immediately after the first bird arrived at the feeder (i.e., bout start). While recording, the observer actively looked for color-ringed individuals within the group. When a color-ringed individual was spotted, the observer followed its movement with the camera to record multiple feeding events of this individual. During the same foraging bout the observer continuously scanned and recorded the foraging activity of all the color-ringed individuals spotted, trying to maximize the number of individuals and feeding events recorded within a bout. Recording was stopped when the group left the feeder (i.e., bout ended). In the Garden recordings were made from a camouflaged hide set up at approximately 5 m from the feeder. On Campus recordings were made without using a hide, but from a distance of approximately 15 m, that assured recording the foraging behavior of the birds without causing any visible disturbance. As the feeder on Campus was located in an area highly frequented by pedestrians (i.e., near a sidewalk), birds using this feeder were well habituated to people. Each recording was made by 1 of 3 observers (A.F., Z.N., or Z.B.) using a digital video camera (Panasonic HC-V510) mounted on a tripod. When no recordings were performed, the feeding platforms were used under the ad libitum feeding regime.

We analyzed every foraging bout separately, as follows. First, we noted the feeder ID where the foraging bout was recorded, and the date and time of the start of the bout. Then, within the bout we first identified all the foraging color-ringed individuals and recorded the following details about every feeding event of each marked individual separately: individual ID, time of the feeding event elapsed from the beginning of foraging bout, density of individuals around the focal individual in the moment of first peck, and social foraging tactic use (producing or scrounging; see below). Density of individuals was calculated as the number of visible tree sparrow individuals divided by the area of the feeder visible in the moment of the peck from the same video frame. To measure the size of this visible area, we used the grid of holes as a reference.

Social foraging tactic use was categorized into 2 types according to Liker and Barta (2002): producing (i.e., finding) and scrounging (i.e., joining). Briefly, we considered a feeding event as scrounging when the focal individual foraged at a hole that was already occupied by another feeding bird in the moment of arrival of the focal individual. Alternatively, we considered a feeding event producing when the focal individual foraged at a hole that was unoccupied by any other bird, that is, no birds were present within 10 cm (i.e., 1 hole distance) of the respective hole. All videos were analyzed by the same person (B.K.).

In total, during the 2 wintering seasons, we recorded 4933 feeding events of 37 individuals (15 males and 22 females; range: 3–401 feeding events per individual, mean = 133.32, median = 113,

SD = 110.96) during 628 foraging bouts. The sex ratio of individuals recorded was not associated with personality test protocol types (protocol 1: 4 males and 6 females; protocol 2: 11 males and 16 females; chi-squared test: $\chi^2 = 0.00$, df = 1, $P = 1$), indicating that protocol types may not bias our results.

Statistical analyses

All calculations and statistical analyses were performed in the R statistical environment version 3.4.4 (R Core Team 2018).

Repeatability of exploration

The exploration score of the individuals was calculated as follows. First, for each individual, we have separately calculated the following variables: "movement latency" (s), expressed as the time elapsed between the first landing of the focal individual after its release into the test room and its first movement; cumulative "number of movements" performed during the test, that is, the sum of the number of hops, flight-assisted hops, and continuous flights; and propensity to explore the test room, expressed through 2 variables, the "number of different compartments visited" at least once during the test (range: 1–8), and the "total number of positions switches between compartments." Second, to determine the relationship between these 4 variables and to reduce the number of variables, we performed a principal component analysis (PCA; "prcomp" function in R). Prior to performing the PCA, variables were rank transformed to improve their distribution. Results of the PCA indicated that only the first principal component, PC1, had an eigenvalue larger than 1 and explained 65.95% variance. PC1 strongly and positively correlated with variables "number of movements" ($r = 0.72$), "number of different compartments visited" ($r = 0.88$), and "total number of position switches between compartments" ($r = 0.68$); and strongly negatively correlated with the variable "movement latency" ($r = -0.71$). Because PC1 explained the largest proportion of the variance, we used predicted PC1 scores as individual exploration score in the subsequent analyses. Note that higher PC1 scores indicate a higher exploratory capacity of individuals. For all individuals, we used the PC1 score of the first exploration test in the statistical analyses.

We tested the repeatability of the exploration score using a linear mixed-effects model (LME) with Gaussian error distribution ("lmer" function in R, package "lme4"; Bates et al. 2015) on a data set that included all individuals tested for exploration. The full model contained the exploration score of the individuals, included as a response variable, sex (male or female), run (first, second or third), protocol type (protocol 1 or 2), and whether the bird was stimulated to enter (yes or no) were entered as fixed factors. Test date (expressed as Julian date; day 1 = 1st October), test time (expressed in minutes from midnight), and bag time (expressed as minutes birds spent in bird bag before the test; see above) were inserted as continuous predictors. Additionally, individual ID was entered as a random factor in the model. Prior to entering into the model, exploration score of the individuals and all continuous predictors were Z-transformed to have mean = 0 and SD = 1 using the "scale" function in R (Schielzeth 2010). Interactions were omitted due to the low sample size for several factor level combinations. We simplified the full model in a stepwise manner using the "drop1" function in R by sequentially removing variables with nonsignificant effects ($P > 0.05$), until reaching the minimal adequate model that included only significant effects. Significance level (P) of the predictors from the minimal model was tested using

the "Anova" function (type III) from the R package "car" (Fox and Weisberg 2011). Repeatability of exploration (r), the associated standard error (SE), 95% confidence intervals (95% CI) and the afferent significance levels (P and P_{perm}) were calculated for the minimal model following Nakagawa and Schielzeth (2010) using the R package "rptR" (Stoffel et al. 2017) with 9999 parametric bootstraps (for the 95% CI) and 9999 permutation steps (for P_{perm}). We note that the repeatability of exploratory behavior calculated on the full model ($r = 0.443$, SE = 0.103, 95% CI = 0.288–0.688, $P < 0.001$, $P_{perm} = 0.006$) resulted similar values as the minimal model (see Results).

Social foraging analyses

We tested the relationship between exploratory behavior and social foraging tactic use by using a generalized linear mixed-effects model (GLMM) with binomial error distribution ("glmer" function in R) on the database of feeding events. We entered social foraging tactic use (producing or scrounging) as a binary response variable in the models. Sex was set as a fixed factor. Date (expressed as Julian date; day 1 = 1st January) and time (expressed in minutes from midnight), density of individuals (see above), and the time of the feeding event within the foraging bout (expressed in seconds passed from the start of the foraging bout) were entered as continuous predictors in the models. Furthermore, 2 individual phenotypic traits were included also as continuous predictors: bib patch size and exploration score. Prior to entering into the models, continuous predictors with a skewed distribution were transformed (i.e., density was square-root transformed, time of the feeding event within the foraging bout, and bib patch areas were log-transformed), and all continuous predictors were Z-transformed to have mean = 0 and SD = 1 (Schielzeth 2010). Individual ID and foraging bout ID were entered as crossed random terms. Since the feeder from the Garden was observed in both years, but the Campus feeder only in the second year, feeder ID was entered in the model as a nested random factor under study year to account for the potential effect of feeder location and year.

The full model, that included all the fixed predictors and the 2-way interactions between the fixed factor "sex" and the continuous variables (i.e., sex was part of each interaction), was simplified in a stepwise manner using the "drop1" function in R by sequentially removing variables with nonsignificant effects, until reaching the minimal adequate model that included only significant predictors (nonsignificant main effects were retained if they were parts of significant interactions). Posthoc comparisons of the different factor levels or slopes of the continuous predictors involved in interactions were tested using the R package "lsmeans" (functions "lsmeans" and "lstrends" in R; Lenth 2016). P value adjustments were performed as implemented by default in the R package "lsmeans." The GLMM analysis was performed using the R package "lme4" (Bates et al. 2015) and significance level of the predictors from the minimal model was tested using the "Anova" function (type III) from the R package "car" (Fox and Weisberg 2011).

Ethical note

Tree sparrows were trapped and handled using standard noninvasive ornithological methods and were released at the site of their capture as soon as it was possible. Birds that were temporarily housed in the outdoor aviary were fed ad libitum with a food mixture consisting of ground corn, barley, millet, and sunflower seeds, which was supplemented with a boiled egg every second day to cover the

Table 1

Results of the generalized linear mixed-effects model presenting the effect of significant predictors on the probability of scrounging from the minimal adequate model (see Methods for details)

	Estimate	SE	z	χ^2	df	P
(Intercept)	−0.970	0.190	−5.109	26.102	1	**<0.001**
Sex (female)	−0.169	0.174	−0.974	0.948	1	0.330
Exploration	−0.046	0.113	−0.407	0.166	1	0.684
Feeding event time within the foraging bout	0.151	0.056	2.699	7.284	1	**0.007**
Density	0.606	0.045	13.380	179.023	1	**<0.001**
Sex (female) × Exploration	0.406	0.168	2.422	5.866	1	**0.015**

For the main effect of the fixed factor "Sex," males are included in the intercept, and therefore, the reported estimates show the extent to which females differ from males. The sign of estimates indicates the direction of associations. Significant effects ($P \leq 0.05$) are highlighted in bold.

birds' protein intake needs (e.g., Pap et al. 2011). Fresh water was provided daily. No birds died in captivity and all birds were released in visibly good health. Tree sparrows were ringed under a license from the Hungarian Bird Ringing Center (license nr. 390 accredited to Z.B.) and permission for the study was granted by the Hajdú-Bihar County Governmental Office, District Office of Debrecen—Department of Environmental and Nature Protection (permit nr. HB/10-KTF/00487). The study complies with the European laws regarding animal welfare and adheres to the ASAB/ABS guidelines for the use of animals in behavioral research.

RESULTS

Repeatability of exploration
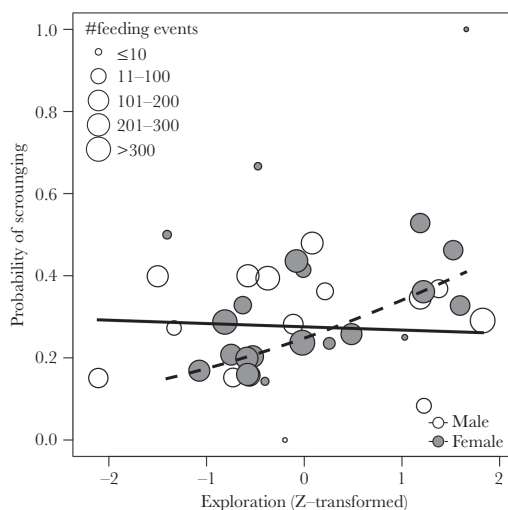
We found that exploratory behavior in tree sparrows was significantly repeatable ($r = 0.455$, SE = 0.105, 95% CI = 0.253–0.669, $P < 0.001$, $P_{perm} = 0.002$), indicating the presence of consistent individual differences in behavior (i.e., personality). In addition, exploratory behavior was significantly influenced by run ($\chi^2 = 30.005$, df = 2, $P < 0.001$), that is, birds were less exploratory during their second personality test ($\beta = −0.642$, SE = 0.125, $t = −5.151$, $P < 0.001$), when compared with the first one. Posthoc comparisons for the third run were not performed due to low sample size ($N = 3$). Furthermore, exploration scores were significantly positively related to the time birds spent in the bag before the personality test ($\beta = 0.292$, SE = 0.056, $t = 5.177$, $\chi^2 = 26.799$, df = 1, $P < 0.001$). None of the other predictors included in the initial model were related to the exploratory behavior of tree sparrows (all $P > 0.05$; results of the full model are presented in the Supplementary Table S1).

Social foraging

We found that the probability of scrounging was related to the exploratory behavior of individuals in a sex-dependent manner (Table 1; Figure 2): probability of scrounging was unrelated to exploratory behavior in males ($\beta = −0.046$, SE = 0.113, $z = −0.407$, $P = 0.684$), but was significantly positively related in females ($\beta = 0.360$, SE = 0.123, $z = 2.918$, $P = 0.003$). Furthermore, density (Figure 3) and time of feeding event within the foraging bout (Figure 4) were both significantly positively related to probability of scrounging (Table 1). None of the other predictors or their interaction with sex were significant (all $P > 0.05$; results of the full model are included in Supplementary Table S3).

DISCUSSION

We studied personality and its relationship with the use of alternative social foraging tactics in free-living tree sparrows while

Figure 2

Sex-dependent association between probability of scrounging and exploratory behavior in free-living Eurasian tree sparrows (*Passer montanus*). Values describing exploratory behavior are Z-transformed (i.e., scaled to a mean of 0 and standard deviation of 1). Symbols show the proportion of scrounging, that is, the number of scrounging events divided by the total number of feeding events per individual; symbol sizes are proportional to the number of feeding events recorded per individual. Lines are logistic regression lines predicted by the minimal adequate model (see Methods).

controlling for a set of potentially confounding variables. We found that tree sparrows behaved consistently during the widely used open-field test measuring exploratory behavior, confirming in this species as well individual personality. We found no sex differences in exploration and modifying the testing protocol did not confound individual behavior during the exploration test. Exploratory behavior, however, seemed to be positively affected by the time birds spent in the bird bag before the test (i.e., individuals that spent a longer time in the bag being more exploratory). This finding confirms results of earlier studies showing that personality and stress responsiveness appear to be linked and the behavior measured during the open-field test (i.e., exploration) incorporates to some extent individuals' coping capacity with stress (Koolhaas et al. 1999; Cockrem 2007; Carere et al. 2010; Coppens et al. 2010). In a social foraging context, we found that females with higher exploration scores scrounged more; however, in males social foraging tactic use and exploratory behavior were not related. Furthermore, density of
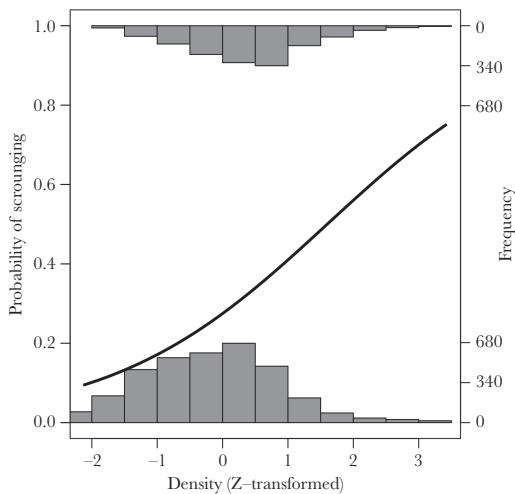
Figure 3
The relationship between the density of individuals (number of individuals per unit area) and probability of scrounging in free-living Eurasian tree sparrows (*Passer montanus*). Values describing density of individuals are Z-transformed (i.e., scaled to a mean of 0 and standard deviation of 1). The line is the logistic regression line predicted by the minimal adequate model (see Methods). Histograms show the frequency distribution of density values separately for producing and scrounging events.
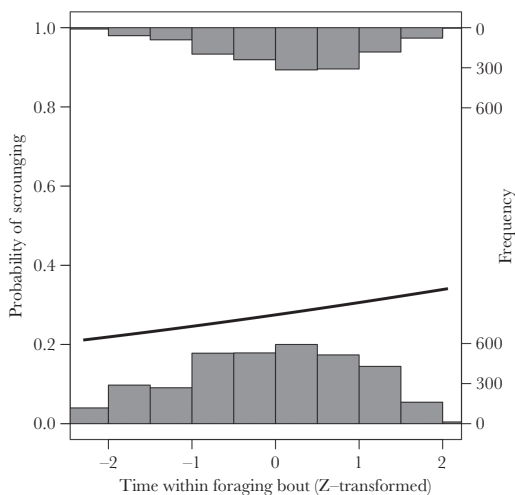
Figure 4
The relationship between the time of feeding event (i.e., producing or scrounging) within the foraging bout and probability of scrounging in free-living Eurasian tree sparrows (*Passer montanus*). Values describing the time of feeding event within the foraging bout are Z-transformed (i.e., scaled to a mean of 0 and standard deviation of 1). The line is the logistic regression line predicted by the minimal adequate model (see Methods). Histograms show the frequency distribution of time of feeding event values separately for producing and scrounging events.

individuals was positively associated with probability of scrounging and feeding later within a foraging bout increased the probability of scrounging.

Exploratory behavior was sex-dependently related to social foraging tactic use; it was positively linked to scrounging in females, but not in males. This result, at least in females, is in line with our first prediction, indicating that more exploratory individuals prefer scrounging. Proactive individuals, which are considered more exploratory, although tend to explore larger areas within a shorter time, are more superficial when gathering information in their environment and in general motivated to receive immediate payoff on their actions (Koolhaas et al. 1999; Coppens et al. 2010). Therefore, in a social foraging context, it seems that proactive individuals indeed favor a foraging strategy which provides a fast benefit (i.e., scrounging). In contrast, reactive individuals, which are usually less exploratory, are more thorough in gathering environmental knowledge and motivated to a lesser extent for a fast reward (Koolhaas et al. 1999; Coppens et al. 2010). Hence, it appears that reactive individuals actually produce more. Our findings on the relationship between personality and probability of scrounging, however, are in contrast with some of the few studies conducted on this topic on other avian models (Kurvers et al. 2010; David et al. 2011; Aplin and Morand-Ferron 2017; but see Jolles et al. 2013). The reason for this discrepancy is not clear. It is now evident from studies on various species that individual personality and group-level (i.e., collective) behavior are interrelated in multiple contexts (Magnhagen and Staffan 2005; van Oers et al. 2005; Webster et al. 2007; Schuett and Dall 2009; Aplin et al. 2014; Pruitt and Keiser 2014; Wright et al. 2015; Jolles et al. 2017; reviewed by Webster and Ward 2011). The mechanisms how the 2 levels of behavior are interacting might, however, be species-specific (e.g., Modlmeier et al. 2014, Lichtenstein and Pruitt 2015). Similar specificity in relational patterns in birds might result in differences between our findings and previous studies.

It remains an open question why social foraging tactic use appears to be differently linked to exploratory behavior in males and females. A possible explanation for this phenomenon might be related to sex-specific differences in trait correlations shaped by sexual and sex-specific selection (Schuett et al. 2010; Immonen et al. 2018). Recent investigations of the evolutionary causes and mechanisms of sex differences in personality traits suggest that sexual dimorphism in personality and its correlations largely arise as a result of sex-specific selection on them (Wyman et al. 2013; see Hämäläinen et al. 2018). Mechanistically, trait correlations may become established in a population either by physical linkage of alleles, pleiotropy, or correlational selection on unlinked alleles, which influence, for example, different neuroendocrine pathways. Sex steroids and their receptors have been found to play an important role in mediating sex-specific trait covariances (Immonen et al. 2018). For example, genetic variation in estrogen receptor α is responsible for the linkage between plumage coloration and sexually dimorphic polymorphism in reproductive behaviors in the white-throated sparrow (*Zonotrichia albicollis*; Horton et al. 2014; Tuttle et al. 2016). Similarly, sex-specific differences in the relationship between personality and social foraging tactic use in males and females might be the result of sex-specific selection on correlated physiological pathways in our tree sparrow population as well. Although this explanation sounds plausible, it is rather speculative, and sex differences in the relationship between personality and social foraging tactic use should be further investigated.

Increasing density of individuals (i.e., decreasing distance between individuals) was linked to an elevated probability of scrounging. This result is in accordance with what we expected based on the predictions of a theoretical model (Barta et al. 1997) and findings of previous empirical studies (Flynn and Giraldeau 2001; Mónus and Barta 2008). However, this relationship can be interpreted in 2 ways in terms of causality. On one hand, our measure of density indicates the compactness of the foraging group, as it reflects the number of individuals per unit area. Therefore, we can assume that the physical closeness of individuals to each other within a foraging flock would result in an increasing opportunity for the individuals to scrounge. On the other hand, individuals with a higher scrounging tendency might intentionally forage closer to conspecifics to increase their chance to scrounge. Hence, this would result in higher density of individuals in groups containing a high proportion of scroungers.

Feeding later within a foraging bout increased the probability of scrounging. This finding is in line with what we intuitively anticipate, since with the advancement of time within a foraging bout both the number of individuals present on the feeding platform and the number of holes discovered are expected to increase due to the sequential arrival of individuals on the feeder. Both factors are favoring the use of scrounging technique against producing and indeed that is what we found. Previous studies found similar relationship between arrival rank on feeder and proportion of scrounging (Beauchamp 2006; David et al. 2011).

Contrary to our expectation we failed to detect a significant relationship between bib patch size—used in this study as a surrogate for dominance status (Mónus et al. 2017)—and probability of scrounging (e.g., Liker and Barta 2002; Lendvai et al. 2006). There are various potential explanations for the lack of association between dominance status and social foraging tactic use. First, assuming that our measure used as a proxy for dominance is valid, our results indicate that in this species the use of social foraging tactics is not significantly influenced by social dominance. Alternatively, if the size of the black bib patch is not a universal indicator of dominance status in this species, but instead a context-, group-, and/or population-dependent signal (see Sánchez-Tójar et al. (2018) for a similar example in the closely related house sparrow [*Passer domesticus*]), we might have failed to detect a relationship between dominance and social foraging tactic use during the period of the study, although it may exist in other contexts. Overall, this question requires further investigations.

In conclusion, in this study, we show for the first time in free-living birds that personality is sex-dependently associated with social foraging tactic use. Our results demonstrate that consistent individual behavioral differences are linked to group-level processes in the context of social foraging, thus suggesting that individual behavioral traits have implications for social evolution.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Behavioral Ecology* online.

FUNDING

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Study 3

Sex-specific signalling of individual personality by a mutual plumage ornament in a passerine

ORIGINAL ARTICLE

Sex-specific signalling of individual personality by a mutual plumage ornament in a passerine

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Abstract

The significance of colour signals in species with strong sexual dimorphism and/or elaborated visual ornaments is rather well-understood. Less attention has, however, been devoted to study colour signals in species with weak or no apparent sexual dimorphism. In such species, an interesting possibility arises as both sexes can bear the same colour ornament(s) (i.e. sexes are mutually ornamented), but their signalling value might differ in males and females. We aimed to explore this possibility by investigating the phenotypic correlates of the black bib, a melanin-based plumage ornament, in the Eurasian tree sparrow (*Passer montanus*). More specifically, we studied the sex-dependent relationships between bib size and three aspects of individuals' phenotype: body condition (i.e. size-corrected 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 findings bring important correlative evidence that mutual ornamental traits may have sex-specific signalling value.

Significance statement

The signalling role of elaborated colourful ornaments, that are usually possessed only by males in sexually dimorphic species, is well-established. The function of various colour traits which are borne by both sexes (i.e. mutual ornaments), however, is less obvious. Do they have a signalling value in both sexes? If yes, do they signal the same information in males and females? Or, most intriguingly, can they convey different information in the two sexes? To test these alternatives, we studied the signalling value of the black bib, a melanin-based mutual plumage ornament, in Eurasian tree sparrows (*Passer montanus*). Apart from being correlated with chronic stress in both sexes, bib size was positively related to activity in females but negatively in males. Our results suggest that the information content of the same colour trait in males and females can be different in mutually ornamented species.

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Introduction

Signals are elaborate and costly traits that can function via many modalities, including acoustic (e.g. bird song; Murphy et al. 2008; Nemeth et al. 2012; Baldo et al. 2015), visual (e.g. horns, tusks, various colourful traits; Geist 1966; West and Packer 2002; Tibbetts and Dale 2004; Loyau et al. 2005; Girard and Endler 2014; Graham et al. 2020) or behavioural ones, which combines both acoustic and visual elements (e.g. nuptial dance; McDonald 1989; Lukianchuk and Doucet 2014). Although research in recent decades has accumulated a large amount of information about communication, in

general, and signalling, in particular, the precise indicator value of traits presumably serving as signals, like colourful ornaments of the integument, is still unknown in many species (e.g. Kemp et al. 2012; Pérez-Rodríguez et al. 2017).

Conspicuous colour signals are usually characteristic of males in sexually dimorphic species, and are frequently used as sexual signs to attract females, which typically have more cryptic colouration (Dale et al. 2015). As a consequence of this common asymmetry between the sexes, there has been a strong bias, ever since Darwin (Darwin 1871), in research interest and effort towards studying species with strong sexual dimorphism, and in particular the role of elaborated ornaments in males in the context of sexual selection (e.g. Pérez i de Lanuza et al. 2013; Seddon et al. 2013; Dale et al. 2015). This phenomenon is well-illustrated by the strongly male-skewed sex ratio found in museum collections from all over the world for both birds and mammals (Cooper et al. 2019). As a result, the adaptive role of female ornaments has been overlooked for a long time, and conspicuous female characters were considered purely as a "by-product" of the shared genome (i.e. genetic correlation) between males and females, but without selection acting on these traits in females (Amundsen 2000). Studies from the last decades (e.g. Amundsen and Forsgren 2001; Jawor et al. 2004; Heinsohn et al. 2005; Komdeur et al. 2005; Weiss 2006, Weiss et al. 2009; Griggio et al. 2010; Baldauf et al. 2011; but see Hill 1993), however, provide considerable evidence that female colouration, similar to that of males, can be adaptive and evolutionary persistent in contexts of sexual (e.g. mate choice, mate competition), social (e.g. competition over non-breeding resources) or natural selection (e.g. camouflage against predators) (Amundsen 2000; Clutton-Brock 2007; Rosvall 2011; Tobias et al. 2012).

Colour traits, including those serving as signals, can be structurally acquired (Prum 2006) or pigment-based (e.g. carotenoids, melanins; McGraw 2006a, b). Melanins are the most common pigment molecules found in the vertebrate integument and are of two types, eumelanins and pheomelanins, which are responsible for the brown to black and yellow to reddish-brown colourations, respectively (Ducrest et al. 2008). The central mechanism orchestrating melanin synthesis from amino acid precursors (i.e. tyrosine, cysteine) is the so-called melanocortin system (Ducrest et al. 2008). This system consists of the proopiomelanocortin (POMC) gene that produces four different types of melanocortin hormones (α-, β- and γ-MSH and ACTH) that bind to five different melanocortin receptors (MC1-5R). The main receptor expressed in the integument, thus responsible for colouration, is the MC1R, the other four receptors (MC2-5R) being expressed weakly at the level of skin but having a more important role in other physiological processes in various parts of the body. Overall, the location and hence functions of melanocortin receptors are highly diverse and include skin

pigmentation, energy expenditure, stress response, immune capacity and behaviour (Ducrest et al. 2008; San-Jose and Roulin 2018). Eumelanin and pheomelanin are synthesised in different pathways, and the synthesis is controlled by receptor agonists binding to MC1R (Ducrest et al. 2008).

Melanin-based colouration has been found to covary with several phenotypic traits (reviewed by Ducrest et al. 2008; San-Jose and Roulin 2018). One of the possible reasons for this phenomenon is the pleiotropic effects of the genes (see above) regulating the melanin synthesis ("melanocortin hypothesis"; Ducrest et al. 2008). The melanocortin hypothesis thus provides a good mechanistic framework to set up predictions about associations between eumelanic colouration, physiology and behaviour. For instance, according to the melanocortin hypothesis, more eumelanised individuals, due to a higher melanocortin activity, should have a more balanced energy homeostasis (i.e. lower body mass) and a higher immune capacity (i.e. higher anti-inflammatory capacity, lower oxidative stress levels), and should be less sensitive to acute stress (i.e. lower glucocorticoid-mediated stress response) (Ducrest et al. 2008). Moreover, melanin-based colouration should be also correlated with individual behaviour (e.g. aggressiveness; Ducrest et al. 2008).

Behavioural traits are usually consistent within individuals across time and contexts, and this behavioural consistency is defined as individual personality (Dall et al. 2004; Réale et al. 2007). Personality of an individual often mirrors its physiology as well, the two being interrelated, forming different "coping styles" (Groothuis and Carere 2005; Carere et al. 2010). For instance, individuals with different coping styles are characterised by different levels of glucocorticoid-mediated stress responsiveness (e.g. Koolhaas et al. 1999): proactive individuals have a less elevated stress response in risky situations, while reactive individuals are the opposite (Cockrem 2007). Similarly, the coping style of individuals is also linked to their immunity (Koolhaas 2008; Lopes 2017). Furthermore, coping style is also translated into a specific individual behavioural profile. For example, individuals with a more proactive coping style are usually more active, exploratory, aggressive and bold, while reactive individuals are less active, exploratory and aggressive, and more shy (e.g. Barnett et al. 2012; Thys et al. 2017). Therefore, given that the melanocortin machinery is associated with physiology (e.g. stress responsiveness, immunity), melanin-based colouration is also expected to correlate with some of the individual personality traits (e.g. activity, exploration, boldness, aggressiveness), and indeed, previous studies found correlations in multiple instances (e.g. Mafli et al. 2011; Mateos-Gonzalez and Senar 2012; Fargallo et al. 2014; Schweitzer et al. 2015; Thys et al. 2020; but see Nicolaus et al. 2016). Taking all together, a large body of evidence seems to support associations between melanin-based colouration, physiology and behaviour (reviewed in detail by San-Jose and Roulin 2018; but see e.g. Santostefano et al. 2019). It has to

be noted, though, that correlations between melanin-based colouration and phenotype are not caused exceptionally by gene pleiotropy in the melanocortin system, and several exceptions are known where melanin-based colour variations among individuals (e.g. colour polymorphism) were not explained by the variation of the MC1R gene (e.g. Derelle et al. 2013; Farrell et al. 2015; Riyahi et al. 2015; Corti et al. 2018), suggesting that other mechanisms can also be important.

Melanin-based colouration, by often showing rather complex co-variations with multiple aspects of individuals' phenotype (see above), forms so-called integrated phenotypes (Pigliucci and Preston 2004). Phenotypic integration of colouration can be similar, but can also differ between the sexes, since trait correlations can be shaped by sex-specific selection on life-history profiles and associated physiological (e.g. hormonal) mechanisms (e.g. Stoehr and Kokko 2006; Ketterson et al. 2009), eventually resulting in sex-specific relationships between traits (i.e. stronger phenotypic integration in one of the sexes). For instance, in female fledgling boobies (*Sula dactylatra*), brown patch size on the head and major wing coverts and testosterone levels were both found to be negatively related to boldness, while in males, these traits were not related (Fargallo et al. 2014). A similar pattern of correlations was found in juvenile kestrels (*Falco tinnunculus*) as well between plumage blackness and boldness (López-Idiáquez et al. 2019).

Melanin-based colour traits are exhibited many times as conspicuous visual attributes (e.g. "bagdes of status") which serve as signals in various contexts (i.e. melanin-based signals; Jawor and Breitwisch 2003; McGraw 2008; Roulin 2016). Here, we study melanin-based signalling in the Eurasian tree sparrow (*Passer montanus*), a species which appears fully monochromatic to the human eye (i.e. males and females look completely similar), but being dichromatic outside the colour spectrum visible to humans, according to a study using avian vision modelling (Eaton 2005). Tree sparrows are mutually ornamented (Kraaijeveld et al. 2007), meaning that both sexes are possessing a black throat patch (hereafter "bib") which is a conspicuous eumelanin-based plumage ornament with demonstrated signalling value in social context during the non-reproductive season (i.e. badge of status; Torda et al. 2004; Mónus et al. 2017): in males, bib size seems to indicate fighting success over both males and females; whereas in females, the social status signalling value of the black bib was not confirmed, although it could not have been excluded (Mónus et al. 2017). Other signalling functions of the bib have not been studied. Nevertheless, the continued expression of the black bib in both sexes, especially in the light of that females in several closely related species lack the black bib (Tibbetts and Safran 2009), leaves open the capacity for a signalling value of the bib in females as well, and also for potential sex-specific effects in the signalling role of this plumage trait.

In this study, we aim to widen our knowledge on the signalling value of the black bib in tree sparrows using the melanocortin hypothesis as a framework (Ducrest et al. 2008). Specifically, we investigate by correlative means whether the size of the bib conveys information, apart from dominance status, about the individuals' body condition (i.e. size-corrected 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 an axis of personality, namely activity in a novel environment (used at occasions as synonym for exploratory behaviour; Réale et al. 2007; Carter et al. 2013). Based on the melanocortin hypothesis (Ducrest et al. 2008), we predict a positive relationship between bib size and activity, while we predict a negative relationship between bib size, body condition, cellular innate immunity/inflammation status and chronic physiological stress levels. Since phenotypic integration of melanin-based ornamental traits can be similar or different in males and females, we also explore if trait correlations of the black bib differ between the sexes by exploring various scenarios regarding the sex specificity of the investigated phenotypic relationships (Fig. 1).

Methods

Study site and period

The study was conducted in the Botanical Garden and the Central Campus of the University of Debrecen (Debrecen, Hungary) during the wintering seasons (i.e. between mid-October and mid-March) of 2016/2017, 2017/2018, 2018/2019 and 2019/2020. 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 (Barta et al. 2004; Fülöp et al. 2019).

Field procedures

Field procedures were similar as described in Fülöp et al.'s study (2019). We captured tree sparrows with mist nets (Ecotone, Poland) at bird feeders each winter between mid-October (after the completion of the annual moult) and late January. Upon capture, we marked all the birds with a uniquely numbered aluminium ring and a unique combination of three plastic colour rings to allow individual identification. Furthermore, we recorded standard biometry of individuals: body mass (± 0.1 g with a Pesola spring balance), tarsus length (± 0.01 mm with a digital calliper) and wing length (± 0.5 mm with a ruler). We also took a blood sample (~ 50–150 μl) from the brachial vein to determine sex using molecular methods (see below), since sexes cannot be reliably distinguished on the basis of plumage characteristics and/or biometry alone (Mónus
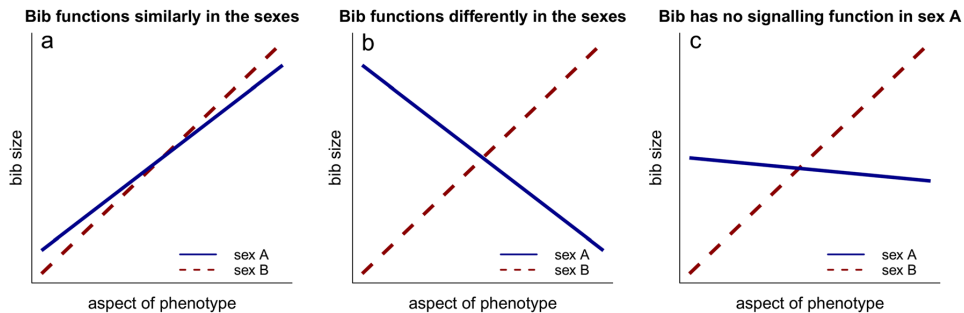
Fig. 1 Predicted relationships between bib size and phenotype in the two sexes under different scenarios. Blue solid and red dashed lines indicate males (sex A) and females (sex B), respectively

et al. 2011). A drop of blood was also used to prepare a blood smear for leukocyte counts (see below). All blood samples were collected within 30 min after capture (mean = 5.33, median = 3.50, SD = 5.67, range = 0–26) to exclude the effect of capture stress on blood cell counts (see e.g. Cīrule et al. 2012). At capture, we also photographed the black bib of the birds with a digital camera near a standard reference for length (i.e. ruler or millimetre paper), while the birds were held in a standardised position with their head facing the camera so that the axis of the beak was perpendicular to the axis of the body and the camera sensor plane (Fülöp et al. 2019). Finally, each individual was tested for activity (see below). After completing all the procedures, individuals were released at the location of their capture.

During the four seasons of the study, we caught 199 tree sparrows in total (70 males and 129 females). A number of individuals which were used to calculate repeatability of activity (see below) were recaptured and underwent again the same procedure as detailed above. The female-biased sex ratio of our sample can be the result of sex-dependent trapability of individuals or can also represent biased sex ratio in the population (i.e. random sample). Evidence from another population (Kato et al. 2017) shows that in tree sparrows, the mortality of male embryos during incubation can cause a similar female-biased adult sex ratio, as observed in our population. Therefore, we are reasonably confident that our sample is random, but we are aware that a sampling bias caused by different trapping probability of males and females cannot be excluded completely. Also, it was not possible to record data blind because our study involved focal animals in the field. However, we minimised eventual observer bias in our data as the analysis of the materials and samples collected during fieldwork was carried out by different persons (see below) without prior knowledge on individuals.

Activity test

The activity of individuals was tested in a mobile test cage, a field-adapted version of the standard open-field test used to quantify exploratory behaviour (see Stuber et al. 2013).

Nevertheless, we prefer to label the behaviour measured in this mobile test cage "activity", since we believe that due to the rather small size of the test cage (see below), the test is more suitable to measure the general level of activity of the individuals rather than exploratory tendency. Moreover, considering also that the behavioural test was carried out at capture, we consider that this measure adequately mirrors the behavioural (acute) stress response of individuals to a risky life event (i.e. trapping; e.g. Martins et al. 2007; Baugh et al. 2013; but see Baugh et al. 2012). It has to be noted though that "activity" and "exploration" are frequently measured using the same test (i.e. open-field test), and the two terms are often used as synonyms (Réale et al. 2007; Carter et al. 2013). The test cage was a 75 × 45 × 55 (L × W × H) cm solid wooden box of which the front wall (75 × 55 cm) was made of transparent wire mesh. The inside space of the test cage was divided into six equal-sized virtual compartments in two rows and three columns which were marked by reference lines traced on the inner walls of the test cage. Three of these virtual compartments (the two upper corners and the lower middle one) contained a perch for each. Individuals were released into the test cage directly from the hands of an experimenter. The behaviour of individuals in the test cage was then video-recorded for 5 min using a video camera (Panasonic HC-V510), which was mounted on a tripod and placed at a distance of 1 m from the wire mesh wall of the cage. While the behaviour of the focal individual was recorded, the experimenter waited quietly on the opposite side of the test cage without disturbing the tested individual. For the same reason, in all seasons, except in 2016/2017, the test cage was visually isolated from the surrounding environment using a camouflage tent, which was installed behind the camera in the front of the cage. The presence or absence of the tent was taken into account during the statistical analyses (see below).

The activity level of individuals was quantified from the video recordings using the "mwrap" event recorder software (Bán et al. 2017). The activity score of each individual was expressed as the total number of position switches between the six compartments of the test cage. We note that,

although not all the compartments contained perches, birds also frequently used the bottom and the wire mesh wall of the cage to land. Therefore, the number of perches seemingly did not influence the activity pattern of individuals in the test cage. Cases when the bird transited a compartment, but did not land in it (e.g. the upper middle part of the test cage while moving from one upper corner to the other), were also counted as position switches. In total, between 2016 and 2020, we tested 167 individuals (56 males and 111 females) for activity, out of which 23 individuals (6 males and 17 females) were tested more than once (21 individuals twice and 2 individuals three times) in order to calculate the repeatability of activity. Repeated tests were performed only on birds that were recaptured on days different from the day of their first capture. Time spent between tests, expressed in number of days, was as follows: mean = 59.28, median = 19, SD = 115.44, and range = 2–379. Out of all ringed individuals, 32 individuals were not tested for activity due to logistical reasons. All videos were analysed by the same person (DL).

Bib size measurements

The bib size (i.e. area) was measured from digital photographs by using the ImageJ software (ver 1.51i for Linux; https://imagej.nih.gov/ij/index.html). For each photo, with the "set scale" function, we first calibrated the unit length on the photograph, using the ruler or the millimetre paper, that was also included in the photograph as a reference. Then, with the "freehand selection tool", we traced the outline of the black bib patch, and measured its area (mm^2) using the "measure" function. The bib area for each individual was measured from the same photo twice, and the values were averaged to increase measurement precision (Fülöp et al. 2019). Repeatability between these two measurements was high (intraclass correlation coefficient, performed with the "ICC" package for R (Wolak et al. 2012; R Core Team 2020): ICC = 0.913, 95% CI = 0.888–0.933, $N = 192$). Bib areas were all measured by the same person (AF).

Leukocyte counts

The number of leukocytes (i.e. white blood cells; WBC) was counted from blood smears following the method described in Pap et al. (2011). Briefly, blood smears were air-dried, then fixed and coloured using Dia-Fix, Dia-Red and Dia-Blue Panoptic (Diagon Ltd., Hungary). Afterwards, five different types of white blood cells (i.e. heterophils, lymphocytes, monocytes, eosinophils and basophils) were identified and counted under a microscope at × 1000 magnification. Total WBC was expressed as the total number of leukocytes per 10,000 erythrocytes after counting in total 50 leukocyte cells. For the statistical analyses, we used two parameters calculated

from leucocyte counts, the total WBC and the ratio of heterophils to lymphocytes (H/L ratio). Total WBC level indicates the cellular innate immune capacity and inflammation status of the organism (Norris and Evans 2000; Salvante 2006), whereas H/L ratio reflects chronic physiological stress (Davis et al. 2008; Davis and Maney 2018). H/L ratios have been found to correlate with the intensity of glucocorticoid-mediated acute stress response (i.e. corticosterone level; Goessling et al. 2015), however, while corticosterone level tends to decrease over time, even if the stressor persists, the H/L ratio seems to remain stable or to even increase (Davis et al. 2008; Goessling et al. 2015; Davis and Maney 2018). Therefore, H/L ratio is a more robust marker of chronic physiological stress, resulting especially from ecological stressors (e.g. hunger, parasites; Davis et al. 2008; Goessling et al. 2015; Davis and Maney 2018). Counts were highly repeatable based on a subset of blood smears chosen at random and counted twice (WBC: ICC = 0.911, 95% CI = 0.792–0.963; heterophils: ICC = 0.931, 95% CI = 0.837–0.972; lymphocytes: ICC = 0.904, 95% CI = 0.779–0.961; H/L ratio: ICC = 0.912, 95% CI = 0.795–0.964; $N = 20$ for each test). All leukocyte counts were carried out by the same person (PIF).

Molecular sexing

Blood samples were stored without any cryoprotectant at − 20 °C until molecular analyses. DNA was extracted by homogenising 5 μl of blood in 150 μl extraction buffer following the protocol described in Bereczki et al. (2014). Molecular sexing was carried out using the 2550F and 2718R primers (Fridolfsson and Ellegren 1999) following the amplification protocol in Bereczki et al. (2014). PCR products were loaded on a silver-stained polyacrylamide gel. The electrophoresis buffer systems and running conditions as well as the staining solutions were used according to Bereczki et al. (2005, see Appendix 2, 4a) and An et al. (2009). The identification of different genders was executed based on the banding pattern after visualisation by white light. Molecular sexing was performed by JB and by a laboratory technician (V. Mester).

Statistical analyses

All calculations and statistical analyses were performed in the R statistical environment version 4.0.3 (R Core Team 2020).

Repeatability of activity level We tested the repeatability of the activity scores using variance partitioning with a linear mixed-effects model (LMM) with Gaussian error distribution ("lmer" function in R, package "lme4"; Bates et al. 2015) as recommended by Nakagawa and Schielzeth (2010). We built a full model that contained the activity score of the individuals as a dependent variable. Sex (male or female) was entered as a fixed

factor in the model, while body condition, test date (expressed as the number of days since 1 October of each wintering season), test time (expressed in minutes from midnight) and handling time (expressed as minutes elapsed from capture until the start of the activity test) were included as continuous predictors. Additionally, all second-order interactions of the fixed factor "sex" and other predictors were tested. Individual ID and season were entered as crossed random factors in the model. Since the effect of the tent cannot be statistically separated from the effect of season (i.e. the tent was not used in the first wintering season, but was used in all other seasons), we accounted for the presence or absence of the camouflage tent in the model through the random factor "season". Body condition was characterised using the scaled mass index (SMI; Peig and Green 2009), which is a size-corrected body mass index. SMI was calculated using the body mass and tarsus length data of individuals with the formula: SMI = body mass × (mean body mass of the sample/tarsus length)$^\wedge b_{SMA}$, where b_{SMA} is the slope of a model II standard major axis regression of log mass on log tarsus length, calculated from the sampled individuals ("lmodel2" function in R, package "lmodel2"; Legendre 2018). The activity score of the individuals, and all the continuous predictors included in the model, except SMI, were first square root–transformed to improve their distributional properties and then Z-transformed (to have mean = 0, SD = 1) to help model convergence (Schielzeth 2010). The full model was simplified in a stepwise manner (using the "drop1" function in R) by sequentially removing terms with non-significant effects ($P >$ 0.050), until reaching the minimal adequate model that included only significant interactions, significant main effects or main effects involved in significant interactions. Significance level (P) of the predictors from the minimal model was tested using the "Anova" function (type II) from the R package "car" (Fox and Weisberg 2019). Post hoc comparisons between different slopes of continuous predictors involved in significant interactions from the minimal model were performed using the R package "emmeans" (function "emtrends"; Lenth 2020). The repeatability of activity (i.e. adjusted repeatability; r), the associated standard error (SE), 95% confidence intervals (95% CI) and significance levels (P and P_{perm}) were calculated following Nakagawa and Schielzeth (2010) using the R package "rptR" with 4999 parametric bootstraps (for the 95% CI) and 4999 permutation steps (for P_{perm}) (function "rptGaussian"; Stoffel et al. 2017).

Bib size and individual phenotypic traits We tested the relationship between bib size and the different phenotypic traits (i.e. body size, SMI, total WBC, H/L ratio and activity) using a LMM with season entered as a random effect with four levels. In this analysis, we used only the data from the first capture of the individuals. Body size index was expressed using predicted values of the first principal component (PC1) extracted using a principal component analysis (PCA; "prcomp" function in R,

package "ade4"; Dray and Dufour 2007) that included three biometry measures of individuals: body mass, tarsus length and wing length. PC1 explained 62.13% of variance and had the following loadings for body mass, tarsus length and wing length, respectively: 0.633, 0.593 and 0.498. Because we are interested in how bib size might integrate information on different aspect of the phenotype, we first built a full model in which we entered bib size as the dependent variable, while sex was set as a fixed factor, and body size index, SMI, activity score of individuals, total WBC and H/L ratio were entered as continuous predictors. The second-order interactions of the fixed factor "sex" with all the continuous predictors were also included in the model. Since the activity of individuals was significantly influenced by a series of confounding effects (see the "Results" section), but also to minimalize eventual collinearity between predictors, we used the residuals of activity scores extracted from the statistical model we used to test the behavioural repeatability as individual activity scores (i.e. residual activity score) in the subsequent analyses. Prior to entering into the models, all variables with a skewed distribution were transformed to improve model fit (bib size was natural base log-transformed, total WBC and H/L ratio were square root–transformed); and both the dependent variable and the continuous predictors were Z-transformed (Schielzeth 2010). The full model was simplified to a minimal adequate model in a similar manner as described above, and the significance level of predictors from the minimal model was tested also in the same way as above presented. The model fit in every case was assessed visually using model diagnostic plots. We note that we omitted one outlier bib size value from the analysis to obtain an adequate model fit (i.e. normality and homoscedasticity of model residuals). Multicollinearity between predictors was excluded as being a potential confounding effect, since all variance inflation factor (VIF) values were less than 5 (e.g. James et al. 2013). Results of both full and minimal models are presented.

Results

Repeatability of activity level Activity was significantly repeatable (adjusted repeatability for the random factor "individual ID", full model: $r = 0.361$, SE = 0.138, 95% CI = 0.216–0.740, $P = 0.001$, $P_{perm} = 0.038$; minimal model: $r = 0.311$, SE = 0.137, 95% CI = 0.116–0.644, $P = 0.004$, $P_{perm} = 0.030$). Activity was significantly influenced by sex, females being less active than males (Table 1). Furthermore, activity was significantly negatively related to the time of the day when the test was performed (Table 1). Finally, activity and SMI were related in a sex-dependent manner (Table 1, Fig. 2), post hoc tests revealing that males with better body condition (i.e. SMI) were less active ($\beta = -0.262$, SE = 0.107, df = 182, $t = -2.443$, $P = 0.016$), whereas in females SMI was not related to activity ($\beta = 0.041$, SE = 0.081, df = 181, $t =$

Table 1 Results of the linear mixed-effects model on the relationship between individual activity and predictors. For the main effect of the fixed factor "sex", males are included in the intercept, and therefore, the reported estimates show the extent to which females differ from males. The sign of estimates indicates the direction of associations. Significance levels indicate results from likelihood ratio tests (ANOVA, type II). Significant effects ($P \leq 0.050$) are highlighted in bold. SMI – scaled mass index (body condition)

Predictors	Full model						Minimum adequate model					
	Estimate	SE	t	χ^2	df	P	Estimate	SE	t	χ^2	df	P
Intercept	0.349	0.269	1.300				0.334	0.256	1.308			
Sex (female)	− 0.353	0.142	− 2.487	4.802	1	**0.028**	− 0.344	0.139	− 2.472	5.455	1	**0.020**
SMI	− 0.290	0.107	− 2.718	0.761	1	0.383	− 0.262	0.106	− 2.480	1.157	1	0.282
Test date	− 0.024	0.113	− 0.212	2.353	1	0.125						
Test time within day	− 0.254	0.123	− 2.062	7.698	1	**0.006**	− 0.145	0.062	− 2.324	5.402	1	**0.020**
Handling time	0.003	0.131	0.023	0.666	1	0.414						
Sex (female):SMI	0.370	0.135	2.746	7.541	1	**0.006**	0.303	0.132	2.295	5.265	1	**0.022**
Sex (female):test date	0.169	0.134	1.263	1.595	1	0.207						
Sex (female):test time within day	0.085	0.143	0.594	0.353	1	0.552						
Sex (female):handling time	0.079	0.152	0.519	0.269	1	0.604						
Random effects												
Residual variance	0.33						0.41					
Individual ID	0.37						0.31					
Season	0.23						0.21					
$N_{individual\ ID}$	167						167					
N_{season}	4						4					
Observations	192						192					

0.507, $P = 0.612$). Test date, handling time and the interactions of sex with test date, time, and handling time did not influenced activity of individuals (all $P > 0.050$; Table 1).

Bib size and individual phenotypic traits Bib size was significantly larger in male than in female tree sparrows (Table 2, Fig. 3). Bib size was associated with activity (i.e. residual activity) in a sex-dependent way (Table 2), results of post hoc tests indicating that in males, activity was marginally negatively related to bib size ($\beta = − 0.268$, SE = 0.137, df = 147, $t = − 1.957$, $P = 0.052$), but in females the two were positively associated ($\beta = 0.183$, SE = 0.090, df = 146, $t = 2.032$, $P = 0.044$; Fig. 4). Furthermore, H/L ratio was significantly positively correlated with bib size, regardless of sex (Table 2, Fig. 5). Body size, SMI and total WBC were not associated with bib size, either independently of or in interaction with sex (Table 2).

Discussion

We studied the potential signalling value, and its sex dependency, of an eumelanin-based mutual plumage ornament, the black throat patch (i.e. bib), in tree sparrows. We found that bib size was positively related in both sexes to H/L ratio (i.e. ratio of heterophils to lymphocytes), a measure characterising
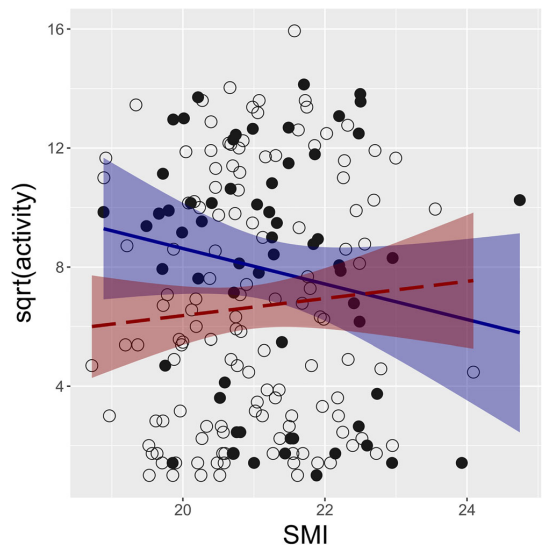

Fig. 2 Sex-dependent relationship between activity (square root) and body condition, expressed through the scaled mass index (SMI), in free-living tree sparrows (*Passer montanus*). Lines and shaded areas are model-predicted logistic regression lines ± 95% confidence intervals. Filled circles and blue solid line indicate males, while empty circles and red dashed line indicate females

Table 2 Results of the linear mixed-effects model on the relationship between bib size and aspects of individual phenotype. For the main effect of the fixed factor "sex", males are included in the intercept, and therefore, the reported estimates show the extent to which females differ from males. The sign of estimates indicates the direction of associations. Significance levels indicate results from likelihood ratio tests (ANOVA, type II). Significant effects ($P \leq 0.050$) are highlighted in bold. SMI – scaled mass index (body condition), total WBC – total number of leukocytes, H/L ratio – ratio of heterophils to lymphocytes

Predictors	Full model						Minimum adequate model					
	Estimate	SE	t	χ^2	df	P	Estimate	SE	t	χ^2	df	P
Intercept	0.451	0.206	2.190				0.438	0.193	2.273			
Sex (female)	− 0.520	0.166	− 3.138	8.372	1	**0.004**	− 0.545	0.157	− 3.470	11.765	1	**0.001**
Body size	0.069	0.119	0.580	1.667	1	0.197						
SMI	0.005	0.138	0.034	0.246	1	0.620						
Activity	− 0.290	0.133	− 2.185	0.401	1	0.527	− 0.268	0.135	− 1.988	0.396	1	0.529
Total WBC	− 0.237	0.121	− 1.958	2.950	1	0.086						
H/L ratio	0.024	0.127	0.185	3.776	1	0.052	0.157	0.075	2.086	4.351	1	**0.037**
Sex (female):body size	0.055	0.156	0.351	0.124	1	0.725						
Sex (female):SMI	0.045	0.165	0.275	0.076	1	0.783						
Sex (female):activity	0.482	0.159	3.023	9.138	1	**0.003**	0.451	0.161	2.791	7.792	1	**0.005**
Sex (female):total WBC	0.176	0.161	1.098	1.206	1	0.272						
Sex (female):H/L ratio	0.188	0.157	1.198	1.434	1	0.231						
Random effects												
Residual variance	0.74						0.78					
Season	0.09						0.08					
N_{season}	4						4					
Observations	146						146					

chronic physiological stress. Interestingly, the relation between bib size and activity was influenced by sex: while males with larger bib patches were less active, females with larger black bib patches were more active. We found no association between bib size and either SMI (i.e. body condition) or total WBC (i.e. cellular innate immune capacity/inflammation status of the organism).

The melanocortin hypothesis provides a series of predictions for trait correlations between eumelanic colouration and individual phenotype (Ducrest et al. 2008). While some of our results may fit into this framework, for a number of phenotypic measures, we found no relationship with colouration. An interesting prediction of the melanocortin hypothesis is that more eumelanic individuals should be more active (Ducrest et al. 2008). The activity level of an individual, as quantified in the present study, might mirror both its physiological state (e.g. acute stress response to capture), but also other aspects of its personality (e.g. exploration, boldness). More eumelanised individuals are expected to be more resistant to acute stress, since melanocortins are involved in the modulation of glucocorticoid-mediated stress response (Ducrest et al. 2008); and more eumelanised individuals have been shown to be more active, exploratory, aggressive and bold (e.g. Mafli et al. 2011; Mateos-Gonzalez and Senar 2012; Schweitzer et al. 2015; Thys et al. 2020; but see Nicolaus et al. 2016). Therefore, we might reasonably expect more eumelanised individuals to be also more active. Our findings apparently
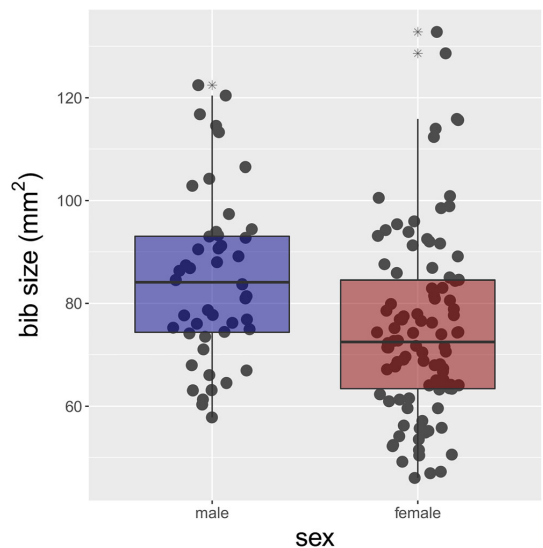

Fig. 3 Boxplot showing the sex differences in bib size in free-living tree sparrows (*Passer montanus*). Horizontal bold lines indicate median values, box margins mark the 25% and 75% quartiles, while whiskers show the lower and upper range values, excluding outliers (i.e. values outside 1.5 times the interquartile range above the upper quartile and below the lower quartile), which are denoted by asterisks. The blue box indicates males, while the red box indicates females. Points denote individual values that are jittered to reduce overlaps of data points on the plot
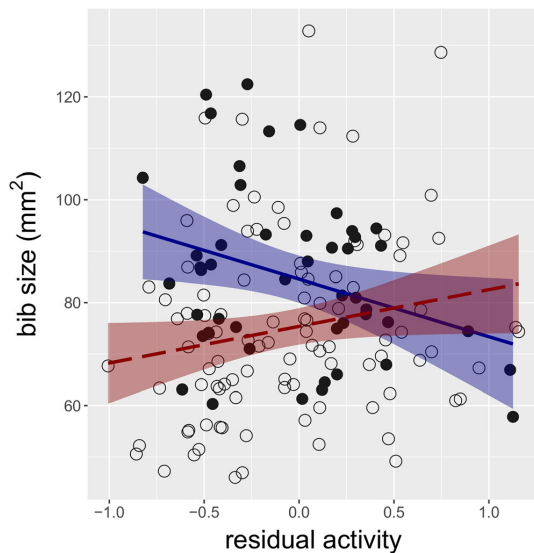
Fig. 4 Sex-dependent relationship between activity (i.e. residual activity) and bib size in free-living tree sparrows (*Passer montanus*). Lines and shaded areas are model-predicted logistic regression lines ± 95% confidence intervals. Filled circles and blue solid line indicate males, while empty circles and red dashed line indicate females

contradict this prediction, at least in part, since we found different relationships between bib size and activity in males and females. The sex-specific relationships between activity and bib size we identified (i.e. negative in males and positive in females) raise several questions. First, what proximate mechanisms might be responsible for this difference between the two sexes? Second, why do females and males advertise their personality differently in this species? In other words, does signalling activity levels differently in the two sexes have an adaptive value?

Phenotypic traits, including colouration, often covary with each other forming integrated phenotypes (Pigliucci and Preston 2004). Mechanistically, covariation between traits is usually the result of a shared physiological mechanism determining trait expression, for instance, when the expression of multiple phenotypic traits is mediated by the same hormone (Ketterson et al. 2009). Hormones, however, can have weaker or stronger effects on the expression of different traits, due to differing circulating hormone concentrations or sensitivity of target tissues, which might result in low or high phenotypic integration (Ketterson et al. 2009). For example, in males and females, trait correlations might be altered by gonadal hormones (e.g. testosterone), which have been found to influence sex-specific trait covariances (e.g. pace-of-life syndrome; Immonen et al. 2018). Melanocortins and sex hormone (e.g. testosterone) production are linked to each other (Ducrest

et al. 2008) and might thus have sex-specific consequences in terms of colour-related trait correlations (e.g. Fargallo et al. 2014). Furthermore, since some hormone levels, for instance that of testosterone, can strongly vary seasonally (e.g. Van Duyse et al. 2003; Laucht et al. 2010), trait correlations mediated by testosterone might also change between seasons and correlational patterns can differ to those reported in this study, which were found during winter.

Why do males and females signal their activity differently? Sex-dependent associations between phenotypic traits, including behaviour, might be the result of adaptations to differences in social context. For instance, in great tits Dingemanse and de Goede (2004) found context-dependent relationship between exploration and dominance (the latter is signalled in great tits by their black "tie"). More dominant territory-holding adults were also more exploratory, while in juvenile, non-territorial birds, the relationship was reversed, with more dominant individuals being less exploratory. Tree sparrows form large flocks during the winter (Summers-Smith 1995; Mónus and Barta 2010); therefore, the most relevant context shaping trait correlations in this species during this period might, at least partly, be related to aspects of social behaviour (e.g. sex roles within the group, social dominance status, group composition). Sex-specific associations between phenotypic traits are already known in this species from previous studies (e.g. dominance signalling, Mónus et al. 2017; determinants of social foraging tactic use, Fülöp et al. 2019), and these suggest that males and females may use distinct behavioural strategies in various social
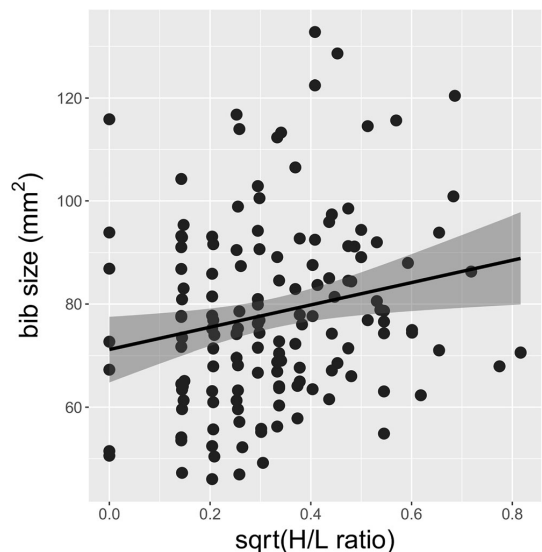

Fig. 5 Relationship between the ratio of heterophils to lymphocytes (square root of H/L ratio) and bib size in free-living tree sparrows (*Passer montanus*). The black line and the shaded area are the model-predicted logistic regression line ± 95% confidence interval

situations. As a consequence, the signalling role of mutual plumage ornaments, and implicitly trait correlations, might evolve in sex-specific ways. Moving beyond, though, the question of why to signal individual personality still remains open. Previously, we have found that personality is related to social foraging tactic use in this species (Fülöp et al. 2019), suggesting that signalling individual personality can be meaningful, at least in this context. Still, we acknowledge that a significant correlation between bib size and activity does not necessarily signify a direct causal link between the two traits and can have other (e.g. genetic) causes (San-Jose and Roulin 2018).

The melanocortin hypothesis also predicts that more eumelanised individuals should have a higher immune capacity (i.e. better anti-inflamatory capacity, more resistant to oxidative stress; Ducrest et al. 2008). We found no relationship between bib size and total WBC (i.e. cellular innate immunity/inflammation status), but found a positive association of bib size with H/L ratio (i.e. chronic physiological stress). H/L ratios adequately indicate individual physiological responses to various internal and/or external stressors (e.g. hunger, parasites; Davis et al. 2008; Davis and Maney 2018) and tend to remain stable over time; thus, H/L ratios mirror long-lasting exposure to stressful stimuli (Davis et al. 2008; Goessling et al. 2015; Davis and Maney 2018). The positive relationship between bib size and H/L ratio is inconsistent with most of the earlier studies (e.g. Minias et al. 2014, 2019; Moore et al. 2015; Svobodová et al. 2018; but see e.g. Svobodová et al. 2013). One possible interpretation of this positive relationship between bib size and H/L ratio is that individuals with large bibs might be involved in a higher number of agonistic interactions which might result in higher physiological stress levels, a cost of social dominance (Davis et al. 2008).

Finally, according to the melanocortin hypothesis, more eumelanised individuals should have a lower body mass, since melanocortins reduce food intake, the amount of adipose tissue, and increase metabolic rate and physical activity (Ducrest et al. 2008). We found no correlation between bib size and body condition (i.e. an index of body reserves). Our results are in contrast with some previous studies reporting either positive or negative relationship between melanin-based colouration and body mass and/or body condition (e.g. Kingma et al. 2008; Roulin 2009; Kim et al. 2013; Moore et al. 2015; reviewed by Roulin 2009, 2016; Guindre-Parker and Love 2014), but are in line with many others where no such relationship was found (e.g. Järvi and Bakken 1984; Jawor et al. 2004; reviewed by Roulin 2009). This diversity of results suggests that the relationship between melanic colouration and condition might not be a simple one (see also San-Jose and Roulin 2018). Indeed, the relationship between body reserves and melanin-based colouration can be confounded by several environmental factors (e.g. food availability; Roulin 2009), but can have genetic bases as well (see discussion in Roulin 2009).

To summarise, our study provides rather intriguing results which bring only a weak support for the melanocortin hypothesis. Although we found significant correlations between activity (i.e. a measure of personality) and eumelanin-based colouration, and chronic physiological stress levels and eumelanic colouration, respectively, both relationships were contrasting to what we predicted based on the melanocortin hypothesis. Several studies seem to support the melanocortin hypothesis (reviewed by Ducrest et al. 2008; San-Jose and Roulin 2018), but some others, similarly to our study, failed to detect expected trait correlations (e.g. Santostefano et al. 2019). Our findings in tree sparrows, however, show that, interestingly, some correlations between melanin-based colouration and individual phenotypic traits might vary according to sex, indicating that the signalling function of melanin traits in males and females might be different, at least in this species. Nevertheless, the role of melanin signals in mutually ornamented species and the mechanisms responsible for the emergence and evolutionary maintenance of sex-dependent signal information content in such species still require further investigations.

Authors' contributions AF and ZB conceived and designed the study. AF, DL, PIF, BK, GC and ZB collected the data. JB performed the molecular sexing. AF and ZB analysed the data. AF wrote the manuscript with significant input from ZB. All authors contributed critically to the drafts and gave final approval for publication.

Data availability The datasets generated and/or analysed during the current study are available from the corresponding author on reasonable request.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

Ethical approval   Tree sparrows were ringed under a licence from the Hungarian Bird Ringing Center (licence nr. 390 accredited to ZB) and permission for the study was granted by the Hajdú-Bihar County Governmental Office, District Office of Debrecen - Department of Environmental and Nature Protection (permit nr. HB/10-KTF/00487-1/ 2016). The study complies with the European laws regarding animal welfare and adheres to the ASAB/ABS guidelines for the use of animals in behavioural research.

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Study 4

Social groups with diverse personalities mitigate physiological stress in a songbird

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Research

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Social groups with diverse personalities mitigate physiological stress in a songbird

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Social groups often consist of diverse phenotypes, including 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 high and low diversity of personality (exploratory behaviour), and found that their physiological state (body condition, physiological stress and oxidative damage) improved with increasing group-level diversity of personality. 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 and might explain the evolutionary coexistence of different personalities in nature.

1. Introduction

Social groups usually consist of a mixture of members with diverse phenotypes [1]. Variation within groups can occur in morphology (e.g. size), behavioural traits (e.g. reactive and proactive behavioural types [2], or social roles (e.g. leaders/followers in human *Homo sapiens* teams [3], or producers/scroungers in tree sparrow *Passer montanus* flocks [4]). Group composition has implications for emergent group-level processes such as decision-making, which ultimately drive group functioning (reviewed in [1,5]). Ethnic diversity can, for instance, have a positive effect on research teams' scientific performance [6].

Personality, the consistent among-individual differences in behavioural phenotype [7], has strong relevance for social life [8]. Social groups can largely differ in their personality composition, some being more homogeneous, while others more heterogeneous [1]. Groups' personality composition can have effects at both the level of the group as a whole (upstream effects) and the level of individual group members (downstream effects). The group-level consequences of groups' personality composition have mostly been assessed in human teams [9,10], where personality composition may affect team performance, albeit in an inconsistent manner [11–13]. In non-human organisms, group personality composition influences within-group social network structure, collective behaviour and group performance [5,14–17]. Although individual-level aspects of sociality, e.g. rank in the dominance hierarchy, have been shown to influence the state of individual members (reviewed by [18,19]), the downstream effects of group behavioural composition on the individual state are surprisingly little

scrutinized [1]. This happens despite social selection theory postulating that the fitness of an individual is contingent upon the phenotype of those with whom it affiliates (i.e. social environment; [15,20]).

Health state can have a strong influence on the individual's social behaviour [21] and, at the same time, is moulded by changes of individual's social environment [19]. Therefore, it is reasonable to assume that physiological condition (e.g. body condition, stress physiology, oxidative damage and immune capacity) of group members is also influenced downstream by the personality composition of their group. Correlative studies on human work teams found that age and gender composition can be associated with subjective self-reported health impairment [22], but human studies with experimental manipulation of group composition and actual health measurements are still lacking. Earlier animal studies mostly assessed how individuals' position within the social structure (e.g. rank in the dominance hierarchy, an individual-level social attribute) affected their health or physiology (reviewed by [18,19]). Experimental studies on animals that tested directly whether group behavioural composition (a group-level social attribute) affects the stress level and condition of group members are very scarce and each involves livestock species [23,24]. No experimental study addressed this question in wild animals.

How could group composition affect the state of group members? Several non-exclusive mechanisms can play a role. Diverse groups provide more opportunities for specialization [1,25] and are more likely to host keystone individuals, which are influential individuals with a disproportionately large effect on other group members and/or overall group functioning [26]. Both role specialization and keystone individuals can lead to superior group-level performance (upstream effect). Indeed, great tit *Parus major* affiliations consisting of diverse personalities show the most effective coordinated action when exploring a habitat patch [5]. Similarly, a mixture of shy and bold guppies *Poecilia reticulata* can be advantageous in reducing the trade-off between exploring novel foraging tasks and antipredator vigilance [16]. The minority of keystone individuals can also substantially affect group-level behaviour and performance [14]. Complementarity of different personalities might also be advantageous in groups of diverse personalities. Stickleback *Gasterosteus aculeatus* shoals solve better a two-stage food acquisition problem when the shoal contains fish that have experience with stage one and fish that have experience with stage two (termed 'experience-pooling'; [27]). Finally, groups with diverse behavioural composition might experience less aggression in pigs *Sus scrofa domesticus* [23]. These group-level advantages of diversely composed groups can bring about higher individual performance (downstream effect) in terms of either fitness or condition [17] by reducing stress exposure and ultimately leaving group members in better physiological condition. Here we asked whether group-level diversity of personalities might influence the physiological state of individual group members.

We conducted an experimental study to explore whether manipulated personality composition of groups *per se* or in interaction with individual personality type affects the physiological condition of group members. Given that diverse groups might have advantages for group functioning (see above) and potentially there is less aggression in behaviourally diverse groups [23], we predicted that individuals in groups with more diverse personality composition would improve their physiological condition as compared with individuals in groups with more homogeneous personality composition. In this case, the improved physiological condition of group members is a legacy of being part of a diversely composed and better functioning group and each group member shares this legacy. We do not know whether this potential benefit is indeed uniform for each member. Alternatively, some members might harvest more the benefits of better group-level functioning to the detriment of other group members. We assessed this prediction by testing whether personality diversity of the groups interacts with individual personality type to influence the physiological condition. A significant interaction might suggest that individuals which either match or mismatch the group's personality composition benefit more than other group members do.

2. Material and methods

(a) Study species

The house sparrow *Passer domesticus* is arguably one of the most popular model organisms in animal ecology and evolution [28]. It is an ideal candidate to study sociality, because it exhibits a wide spectrum of social behaviour including colonial breeding, social foraging or communal roosting [29]. At our study site, house sparrows are year-round residents, breed in cavities of stall buildings at the cattle farm and forage in flocks of various sizes, especially outside the breeding season. Flock sizes vary from small to medium, containing from a few birds up to some dozen individuals, similar to other populations (see [29]).

(b) Study protocol

The study is based on a large sample of 240 house sparrows. The same study protocol was used in six study replicates. We captured 40 sparrows (1:1 sex ratio) per each study replicate (electronic supplementary material, table S1). These 40 birds were divided into four treatment groups (see below) consisting of 10 birds each, which yielded 24 social groups for the entire study (four treatment groups per study replicate × six study replicates). There was no significant difference in sex ratio between the treatment groups in any of the study replicates (χ^2 test, all $p > 0.362$).

The study timeline in each study replicate was as follows. Upon capture (day 0), birds were marked with an aluminium ring, and their sex and body mass was recorded. Then they were housed in indoor aviaries for 18 days at the campus of Babeş-Bolyai University, Cluj-Napoca, Romania. On days 5–7, we recorded exploratory behaviour as a well-established and ecologically relevant axis of personality [30] following the novel environment test of Dingemanse *et al.* [31]. At day 9, we measured the body mass and tarsus length of the birds and took a pre-treatment blood sample. Then the birds were allocated according to an *a priori* defined, stratification based protocol (for details, see the electronic supplementary material) into one of four social treatment groups of 10 birds each: 'random' (random subsample of birds of a given replicate), 'low-exploratory' (only birds with low-exploratory scores), 'high-exploratory' (only birds with high scores) and 'variable' (an equal mixture of birds with either low or high scores) (see details of Social treatment methods in the electronic supplementary material). Social treatment protocol successfully created differences in the mean and variance of exploration score (personality) among groups as recommended by Farine *et al.* [1] (electronic supplementary material, figure S1). The mean exploratory score was the smallest in the low-exploratory group, intermediate in the random and variable groups, and the largest in the high-exploratory group (linear mixed-effects model with study replicate as a random factor, treatment group effect: $\chi^2_3 = 632.92$, $p < 0.001$; electronic supplementary material, figure S1a).

The variance of the exploratory score was the lowest in the low- and high-exploratory groups, intermediate in the random group and the highest in the variable groups (treatment group effect: $\chi^2_3 =$ 401.78, $p < 0.001$; low- versus high-exploratory: $\chi^2_1 = 1.93$, $p = 0.165$; random versus variable: $\chi^2_1 = 58.58$, $p < 0.001$; electronic supplementary material, figure S1b). The significant difference in the variance of exploratory score between the random and the variable groups is owing to the former being an even sample of the entire range of exploratory behaviour, while the latter being a mixture of low-exploratory and high-exploratory individuals in equal proportion (see details of Social treatment methods and the electronic supplementary material, figure S2). Therefore, as an additional characterization of the birds' social environment, we calculated *a posteriori* the Shannon diversity index of exploratory behaviour for each social group of 10 sparrows by dividing exploration values into 10 ordered categories of roughly equal sizes. As expected, the Shannon diversity index was the lowest in the low- and high-exploratory groups, intermediate in the variable group and the highest in the random group (treatment group effect: $\chi^2_3 = 68.118$, $p < 0.001$; low- versus high-exploratory: $\chi^2_1 = 1.30$, $p = 0.254$; random versus variable: $\chi^2_1 = 11.73$, $p < 0.001$; electronic supplementary material, figure S1c).

The social treatment period lasted 9 days until day 18, when we measured again the body mass and took a second blood sample to measure the post-treatment physiological condition. The physiological state was characterized by measuring body condition (scaled body mass index, SMI), heterophil-to-lymphocyte (H/L) ratio, oxidative damage to lipids (malondialdehyde concentration, MDA) and innate immune capacity (natural antibodies—agglutination score; complement system—lysis score) both during the pre- and post-treatment sampling events. These traits were chosen for the following reasons. Changes in body condition usually take more time than changes in other physiological traits. Among the factors that affect body condition, exposure to stress stimuli is known to reduce body condition [32]. Ultimately, impaired body condition can have widespread consequences for the organism. H/L ratio has been shown to correlate with the glucocorticoid stress response governed by the hypothalamic–pituitary–adrenal axis [33,34], but is less sensitive to handling stress as compared with plasma levels of corticosterone (the main glucocorticoid in birds). H/L ratio therefore can indicate the degree of physiological stress. MDA is a versatile marker of oxidative stress for two reasons. MDA indicates the damage to vital cell membrane lipids, which has substantial adverse consequences from the cell level to the organism level. Besides being a direct measure of oxidative damage, MDA is a pro-oxidant itself with a long half-life and hence can reach far from its site of origin damaging other vital macromolecules [35]. Agglutination and lysis capacity of the plasma describes the activity of the humoral innate immune system and hence is an indicator of the first line of defence of vertebrate hosts against invading microorganisms [36]. Higher scores of agglutination and lysis indicate higher innate immune responsiveness. There was no significant difference among social treatment groups in the pre-treatment values of the five physiological response variables (all $p > 0.188$; see detailed statistics in the electronic supplementary material, Additional results). The different physiological variables are weakly correlated both in the pre- and post-treatment samples except for the positive association between agglutination and lysis scores (electronic supplementary material, table S2). We provide a more detailed description of the study timeline, captivity conditions, measurement of exploratory behaviour, assignment to social treatment groups, blood sampling and physiological measurement methods in the electronic supplementary material.

(c) Statistical procedures

The statistical analyses were carried out in the R statistical environment (v. 4.03; [37]). Because we used a repeated-measures approach to analyse our data, each physiological variable contained the values of both sampling events (i.e. pre-treatment and post-treatment values). Each physiological trait was analysed in a separate statistical model. H/L ratio was arcsine square root transformed, malondialdehyde level was log-transformed and exploration score was $\log(x + 1)$-transformed to reduce the bias in their distributions, while agglutination and lysis scores were converted into binary variables (0 for absence and 1 for the presence of agglutination or lysis) because they were highly zero-inflated. To improve model convergence, the continuous dependent variables (i.e. body condition, H/L ratio and MDA) and the continuous predictor variables (exploration score and Shannon diversity) were Z-transformed to have zero mean and unit standard deviation [38].

In the first set of models, we assessed the effect of social treatment and the effect of sampling event × social treatment interaction on the individual physiological responses of sparrows. The explanatory variables were the same in all models as follows: sex (male or female), social treatment (random, variable, high-exploratory and low-exploratory) and sampling event (pre-treatment and post-treatment) were set as fixed factors, and individual exploratory score as a continuous predictor. In addition, all second-order interactions between the four explanatory variables were also tested. Note that, in this set-up, a significant interaction with sampling event indicates that the rate of change in the response variable is influenced by the other explanatory variable in the interaction. Study replicate, treatment group identity (ID) nested within study replicate, and individual ID nested within study replicate and treatment group ID were entered as random factors. We used linear mixed-effects models with normal error distribution (LMMs; 'lmer' function of the R package 'lme4'; [39]) for body condition, H/L ratio and MDA, while we used generalized linear mixed-effects models with binomial error distribution ('glmer' function of the R package 'lme4') for agglutination and lysis scores. The assumption of homogeneity of residual variances among treatment groups were met for each response variable of the LMM models (Levene test, all $p > 0.195$). We assessed the fulfilment of model assumptions by graphical diagnosis; all assumptions were met for each model. Each model was simplified to obtain minimal adequate models (MAMs) containing only significant main effects or their interactions by sequentially dropping predictors with non-significant ($p > 0.050$) effects using the 'drop1' R function. The sampling event × social treatment interaction and its main effects were kept in the model even if they were non-significant because our main interest is related to the sampling event × social treatment interaction.

In the second set of models, we assessed the effect of Shannon diversity of group personality and the effect of sampling event × Shannon diversity interaction on the individual physiological responses of sparrows. For this, we used a similar approach as in the first model set with the only difference that we entered groups' Shannon diversity of exploration as a continuous predictor in the models instead of the fixed effect of social treatment.

The reported significance levels were calculated using type II Wald chi-square tests using the 'Anova' function of the R package 'car' [40]. The post-hoc comparisons of individual changes in physiological variables between the two sampling events as a function of different treatment groups (first set of models) or as a function of groups' Shannon diversity of exploration (second set of models) were conducted using the R package 'emmeans' (functions 'emmeans' and 'emtrends', respectively; [41]). Tables 1 and 2 present the type II ANOVA results of MAMs for the first and second set of models, respectively. Electronic supplementary material, tables S3 and S4 present the parameter estimates of both the full models and the MAMs for the first and second set of models, respectively. All data and analyses code are deposited in the Dryad Digital Repository [42].

Table 1. Minimal adequate models containing predictors of individual responses in physiological state of house sparrows to social treatment. (Statistically significant effects ($p \leq 0.050$) are marked in bold, while marginally significant effects ($0.050 < p \leq 0.100$) in italics. SMI—scaled mass index (body condition), H/L ratio—heterophil-to-lymphocyte ratio (physiological stress response), MDA—malondialdehyde (oxidative damage to lipids).)

response	fixed effects	χ^2	d.f.	p
SMI	sampling event	0.00	1	1.000
	treatment	3.70	3	0.296
	sex	**13.66**	**1**	**<0.001**
	sampling event × treatment	**14.32**	**3**	**0.003**
H/L ratio	sampling event	0.00	1	1.000
	treatment	1.38	3	0.709
	sex	0.02	1	0.879
	sampling event × treatment	*7.56*	*3*	*0.056*
	sampling event × sex	**3.85**	**1**	**0.050**
MDA	sampling event	0.00	1	0.979
	treatment	1.04	3	0.792
	sampling event × treatment	**13.83**	**3**	**0.003**
agglutination	**sampling event**	**12.54**	**1**	**<0.001**
	treatment	1.51	3	0.680
	sampling event × treatment	0.81	3	0.848
lysis	**sampling event**	**16.17**	**1**	**<0.001**
	treatment	*7.09*	*3*	*0.069*
	sampling event × treatment	0.38	3	0.945

Table 2. Minimal adequate models containing predictors of individual responses in physiological state of house sparrows to social treatment in relation to the groups' personality diversity. (Statistically significant effects ($p < 0.050$) are marked in bold. SMI—scaled mass index (body condition), H/L ratio—heterophil-to-lymphocyte ratio (physiological stress response), MDA—malondialdehyde (oxidative damage to lipids).)

response	fixed effects	χ^2	d.f.	p
SMI	sampling event	0.00	1	1.000
	sex	**12.68**	**1**	**<0.001**
	Shannon diversity	1.57	1	0.210
	sampling event × Shannon diversity	**14.44**	**1**	**<0.001**
H/L ratio	sampling event	0.00	1	1.000
	Shannon diversity	0.00	1	0.977
	sampling event × Shannon diversity	0.62	1	0.431
MDA	sampling event	0.00	1	0.983
	Shannon diversity	1.37	1	0.241
	sampling event × Shannon diversity	**6.10**	**1**	**0.014**
agglutination	**sampling event**	**12.36**	**1**	**<0.001**
	Shannon diversity	0.18	1	0.675
	sampling event × Shannon diversity	1.49	1	0.222
lysis	**sampling event**	**16.10**	**1**	**<0.001**
	Shannon diversity	0.02	1	0.882
	sampling event × Shannon diversity	0.10	1	0.756

3. Results

(a) Social treatment effects

In the first model set, we assessed the effects of social treatment on the individual's physiological responses. The sampling event × social treatment interaction was significant for body condition and oxidative damage, and marginally significant for H/L ratio, while it was non-significant for agglutination and lysis (table 1, electronic supplementary material, table S3, figure 1; see also the individual reaction
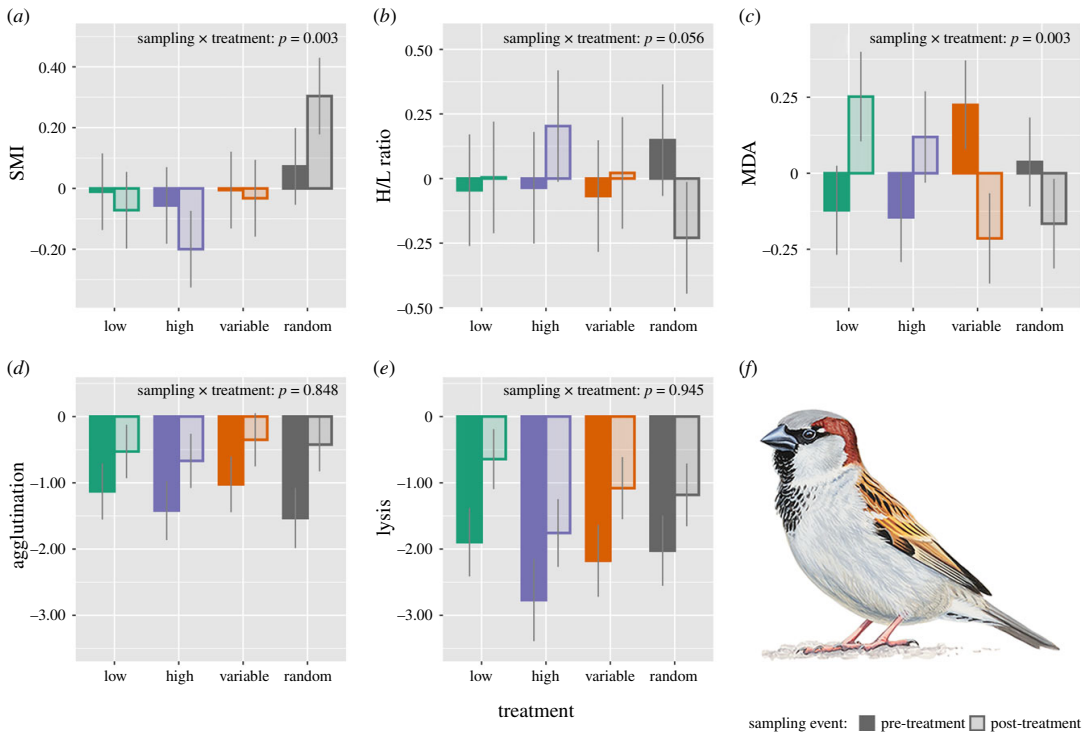
Figure 1. Physiological responses to social treatment: (a) body condition (SMI), (b) heterophil-to-lymphocyte ratio (H/L ratio, an indicator of physiological stress response), (c) oxidative damage to lipids (i.e. malondialdehyde, MDA), and (d–e) constitutive immune capacity, as expressed through agglutination score (d) and lysis score (e). Model-predicted mean ± s.e. are shown for each treatment group both at pre-treatment (dark bars) and post-treatment (light bars) sampling events. (f) Male house sparrow painting credit: Márton Zsoldos. (Online version in colour.)

norms of physiological traits to social treatment in the electronic supplementary material, figure S3). The main effect of social treatment was non-significant for each response variable, except for a marginal effect in case of the complement system of the innate immunity (i.e. lysis score; table 1, electronic supplementary material, table S3). Below we present the results related to the physiological variables for which the sampling event × social treatment interaction was significant.

The improvement in body condition during the treatment period was significantly higher in the random group as compared with the other three groups (see sampling event × social treatment interaction in the electronic supplementary material, table S3a). Post-hoc tests revealed that body condition improved significantly in the random group between the two sampling events ($\beta = -0.232$, s.e. = 0.074, $t_{236} = 3.123$, $p = 0.008$), while body condition was not affected by the experimental treatment in the other three treatment groups (all $p > 0.198$). Body condition increased only in the random group and decreased in the other three groups (figure 1a).

The rate of increase in H/L ratio was significantly higher in the high-exploratory group, and marginally higher in the low-exploratory and variable groups as compared with the random group (see sampling event × social treatment interaction in the electronic supplementary material, table S3b). Post-hoc tests showed a weak decrease in H/L ratio in the random group between the two sampling events ($\beta = 0.378$, s.e. = 0.166, $t_{235} = 2.270$, $p = 0.093$), while it remained unchanged in the other three groups (all $p > 0.484$). H/L ratio decreased

only in the random group, while increased in the other three groups (figure 1b).

The increase in oxidative damage during the treatment period was significantly higher in the low-exploratory group and marginally higher in the high-exploratory group as compared with the random group, while the variable and random groups did not differ (see sampling event × social treatment interaction in the electronic supplementary material, table S3c). The post-hoc tests revealed that individuals from the variable group showed a marginally non-significant decrease in oxidative damage levels between the two sampling events ($\beta = 0.439$, s.e. = 0.179, $t_{233} = 2.452$, $p = 0.058$), whereas birds from the other three treatment groups were not affected by the experimental manipulation (all $p > 0.140$). MDA levels (i.e. oxidative damage to lipids) increased in high- and low-exploratory groups, but decreased in the variable and random groups (figure 1c).

Individuals' personality was not associated with the individual responses in physiological condition by itself or in interaction with social treatment, hence was dropped from the models (table 1, electronic supplementary material, table S3). Constitutive innate immunity improved during treatment as both agglutination and lysis scores increased significantly between the two sampling events, and males had higher body condition than females (table 1, electronic supplementary material, table S3).

(b) Shannon diversity of group's personality
To assess the role of personality diversity of experimental social groups, we tested whether the calculated Shannon
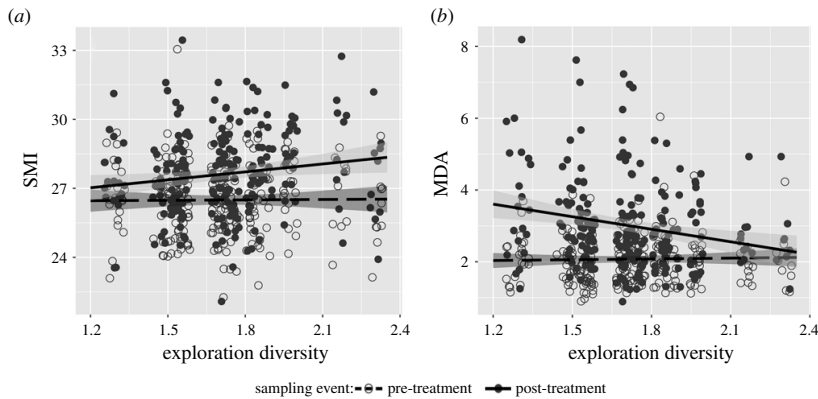
Figure 2. Physiological condition improved in social groups with diverse personalities. Relationships between the Shannon index of group-level personality diversity of house sparrows and individual responses to social treatment in terms of (*a*) body condition (SMI) and (*b*) oxidative damage to lipids (MDA). Open symbols and dashed lines denote the pre-treatment sampling, while the filled symbols and continuous lines denote the post-treatment sampling. Regression lines are model-predicted slopes with 95% confidence intervals (shaded areas). Dots of the same exploration diversity value are jittered to decrease their overlap.

diversity index predicted the individual's physiological responses to social treatment. The sampling event × Shannon diversity interaction was highly significant for body condition and oxidative damage (figure 2), while it was non-significant for H/L ratio and the activity of constitutive innate immunity as measured by agglutination and lysis (table 2, electronic supplementary material, table S4). The main effect of Shannon diversity was non-significant for each response variable (table 2, electronic supplementary material, table S4). Regarding the significant interactions, we found that body condition increased ($\beta = 0.146$, s.e. = 0.067, $t_{24.9} = 2.195$, $p = 0.038$), while oxidative damage to lipids (i.e. MDA) decreased ($\beta = -0.170$, s.e. = 0.067, $t_{66.0} = 2.532$, $p = 0.014$) with increasing personality diversity in the post-treatment sample (i.e. after exposure to social treatment), while these two response variables were unrelated to Shannon diversity in the pre-treatment sample (i.e. prior to social treatment; all $p > 0.413$; table 2, electronic supplementary material, table S4, figure 2). The other three response variables (i.e. H/L ratio and agglutination and lysis) were unrelated to Shannon diversity in either the pre-treatment or the post-treatment samples (all $p > 0.231$ and all $p > 0.578$, respectively).

4. Discussion

In the realm of human psychology, there is a long-standing debate on whether uniformly or diversely composed teams perform better [11,12], but almost nothing is known about whether group behavioural composition affects the physiological condition of group members either in humans or other animals. For instance, pigs housed in groups of uniform behavioural composition or in groups with a mixture of behavioural types did not differ in their glucocorticoid stress response or weight gain [23,24]. By contrast, our results are consonant with the old Latin proverb 'Varietas delectat' [43], as here we showed that body condition significantly improved, H/L ratio (an indicator of physiological stress) was marginally reduced and oxidative damage level was significantly reduced for house sparrows living in a social environment with diverse personalities. Therefore, living in social groups with diverse composition can provide at least short-term benefits in terms

of reduced physiological stress and superior condition. The finding of no significant interactions between social treatment and individual's exploration score suggests that all individuals in diverse groups similarly enjoy these benefits.

The two heterogeneously composed social treatment groups of our study (i.e. 'variable' and 'random' groups) had a higher diversity of personalities than the two homogeneously composed ones (i.e. 'low-exploratory' and 'high-exploratory' groups). Nevertheless, the effect of treatment on body condition and H/L ratio differed between the variable and random groups, as only birds of the random group fared well. This suggests that there is a personality diversity threshold, which has to be exceeded to reap physiological benefits of group composition. Indeed, the heterogeneous variable group only marginally differed from the homogeneous high-exploratory group, while the random group stood out among all groups in terms of personality diversity (electronic supplementary material, figure S1c). Therefore, an equal mixture of low- and high-exploratory birds (i.e. personality extremes) in the variable group is not necessarily sufficient, but a more diverse mixture of the entire range of personalities, like in the random group, is required for some of the individual-level physiological benefits to emerge. A possible explanation for such a threshold effect could be that there is more room for role specialization, keystone individuals and complementarity of different personalities in diversely composed groups [1,25,26], which lead to superior group-level performance (upstream effect) [5,14,16,27] and ultimately precipitate superior individual-level performance (downstream effect) [17]. This hypothesis can be tested by studying how social groups that differ in personality diversity succeed in solving novel tasks (e.g. in a foraging context).

It is important to note that we found a positive effect of social diversity on health in a set-up where a constant amount of food was available. This suggests that the benefits of social diversity might arise because of the type and intensity of aggressive interactions between members rather than being the consequence of more obvious benefits like improved habitat exploration, defence against predators and decision-making. Therefore, preference for bonding with dissimilar individuals (i.e. heterophily), and the resulting better health state of individuals in diverse groups might reinforce the improved group-level

outcomes, creating a positive feedback loop [44] between group-level and individual-level performances. Indeed, affiliations of great tits and simulated social groups consisting of diverse personalities show the most effective coordinated action when exploring a habitat patch (group-level performance) [5], while social groups composed of diverse personalities also improve the physiological condition (individual-level performance; present study). These simultaneous group- and individual-level benefits of diversely composed groups can drive the evolutionary maintenance of heterophily [45].

Consistency of personality traits places a constraint on individuals because one is either more reactive (shy, neophobic, less exploratory, less aggressive) or more proactive (bold, novelty seeking, more exploratory, more aggressive) [2]. However, if different personalities affiliate, they can share mutual benefits; a concept termed social heterosis [46]. Social heterosis in associations of dissimilar personalities thus can explain why behavioural (and genetic) diversity can evolutionarily persist [46]. Negative frequency-dependent selection is another evolutionary explanation for the existence of behavioural polymorphisms (producers–scroungers, hawks–doves and leaders–followers) and has been shown to maintain diversity in group personality composition [47]. Our findings bring evidence to these potential explanations. Living in social groups with diverse composition can provide benefits in terms of reduced physiological stress. Because the physiological state in one life-history stage can have carry-over effects on performance in the subsequent life-history stage (e.g. from wintering to the breeding stage, see e.g. the case of American redstart *Setophaga ruticilla* [48,49]), our results might provide a physiological mechanism that could be responsible for the evolutionary maintenance of behavioural diversity in social groups. These findings, thus, bring helpful insight into the study of social evolution, which is a fundamental question in biology and has implications for human work teams. Although the role of group composition in human team performance is still contentious [10], there is some evidence showing that heterophily is advantageous in project groups that are less stable in time and are engaged in creative tasks, but disadvantageous in production groups that are stable in time and are engaged in routine tasks [12].

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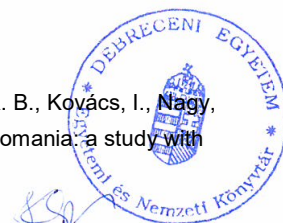# List of publications related to the dissertation

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Total IF of journals (publications related to the dissertation): 11,09

The Candidate's publication data submitted to the iDEa Tudóstér have been validated by DEENK on the basis of the Journal Citation Report (Impact Factor) database.

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