THE EFFECTS OF BEHAVIOURAL FLEXIBILITY ON SOCIAL AND REPRODUCTIVE SUCCESS IN BIRDS

Ph.D. Thesis

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ABSTRACT

In our rapidly changing environment that we share with other animal species, beside our natural curiosity to understand processes in nature, it is also our responsibility to pursue a growing insight into the mechanisms how other species cope with alterations caused by humans. The idea that cognition and behavioural flexibility allow for quick responses to environmental fluctuations, and therefore may play a crucial role in adaptive processes has been brought into the focus of behavioural ecology in the past decades. In my thesis, I investigated the relationship of innovativeness with different proxies of breeding success and with social behaviour in two synanthropic bird species.

In the first part of the thesis, I studied the association between innovativeness and different measures of breeding success in free-living great tits (*Parus major*). Both urban and forest dwelling pairs that solved an obstacle-removal task faster during breeding had higher hatching success and higher number of fledglings. This suggests a positive link between innovativeness and fitness, although this correlation was not detected in another, food-extraction task. Furthermore, I found a positive association between females’ success in the same obstacle-removal task and the occurrence of extra-pair offspring in their broods. At the same time, I found no correlation with extra-pair offspring occurrence and the social father’s problem-solving success. Pairs of two highly neophobic individuals were less likely to have extra-pair offspring in their broods than less neophobic pairs. Collectively, these results suggest that innovativeness may facilitate reproductive success and promiscuity in great tits.

In the second part of my thesis, I showed in captive house sparrow (*Passer domesticus*) flocks that, contrary to our expectations, birds did not interact with flock-mates according to their experimentally manipulated apparent problem-solving success, but according to flock-mates’ actual innovativeness. Innately innovative birds got attacked by their flock-mates more frequently than less innovative birds, but sparrows did not show preference towards innovative individuals when accompanying their conspecifics. This suggests that aggressive scrounging of food (a frequently occurring feeding strategy in sparrows) from innovators is probably more important than the potential benefit of social learning from innovative food-finders.

In the same experiment, I found that permanent visual isolation during the early days of captivity was associated with high mortality of wild-caught house sparrows, which was alleviated by intermittently allowing visual contact. This suggests that visual isolation, which is often needed when studying individual innovativeness, might affect the mortality of social

species and should be applied with caution. Motivated by these findings, I conducted a systematic review of the mortality data on captive house sparrows in the scientific literature, revealing that most publications lack sufficient data on study subjects' survival and housing conditions, including visual isolation regimes.

These results provide some of the first evidence for connections of innovative behaviour with fitness and social behaviour, shedding light on the mechanisms how individual variation in innovativeness may be shaped within a species.

KIVONAT

Gyorsan változó világunkon más állatfajokkal osztozunk, így a természet felé forduló kíváncsiságunk mellett felelősséggel is tartozunk azért, hogy megértsük, miként alkalmazkodnak egyes fajok az emberek által megváltoztatott környezethez. Az utóbbi évtizedekben a viselkedésökológia egyik központi kérdésévé vált annak feltárása, hogy az állatok kognitív képességei, valamint a viselkedési flexibilitás hogyan teszi lehetővé a környezeti változásokra adott gyors válaszokat és az adaptációt. Értekezésemben két, ember közelében élő madárfaj egyedein vizsgáltam az innovatív viselkedés kapcsolatát a szaporodási sikerrel és a szociális viselkedéssel.

Értekezésem első részében vadon élő széncinegék (*Parus major*) populációiban vizsgáltam az innovativitás, valamint a szaporodási siker különböző mérőszámai közötti kapcsolatot. Mind a városi, mind az erdei élőhelyen magasabb volt a kelési siker és a kirepült fiókák száma azokban a fészekaljakban, ahol a szülők gyorsabban oldottak meg egy akadály-eltávolító feladatot. Ebből az innovativitás és a rátermettség közötti pozitív kapcsolatra következtethetünk, bár ilyen összefüggést egy másik, táplálékszerzési feladatban nem találtunk. Az akadály-eltávolító feladatban sikeres tojók fészekaljaiban magasabb volt az extra-pár utódok előfordulási gyakorisága, ugyanakkor a hímek innovativitása nem állt összefüggésben a fészekaljukban talált extra-pár utódok előfordulásával. Az extra-pár utódok előfordulási valószínűsége alacsonyabb volt azokban a fészekaljakban, ahol mindkét szülőnél magas neofóbiát mértem. Mindezek arra engednek következtetni, hogy az innovativitás elősegíti a magasabb szaporodási sikert, valamint a páron kívüli megtermékenyüléseket.

Értekezésem második részében fogságban tartott házi veréb (*Passer domesticus*) csapatokban kimutattam, hogy az előzetes várakozásainkkal ellentétben az egyedek nem a társak látszólagos, kísérletesen manipulált problémamegoldási sikere alapján ítélték meg azok innovativitását, hanem valódi innovativitásuknak megfelelően viselkedtek velük. Az innovatív egyedeket gyakrabban támadták meg a csapattársak, ugyanakkor békés helyzetben az egyedek nem részesítették előnyben az innovatív társak közelségét. Ezekből arra következtethetünk, hogy az innovatív társakkal szembeni viselkedés megválasztásában az agresszív potyázás (egy gyakori táplálékszerzési stratégia) fontosabb lehet a házi verebek számára, mint a társaktól történő tanulás.

Ugyanebben a kísérletben azt tapasztaltam, hogy a fogság első napjaiban alkalmazott állandó vizuális elkülönítés magas mortalitással járt, amit mérsékelt, ha időnként láthatták

egymást a fajtársak. Ezek alapján a problémamegoldás tanulmányozásához sok esetben elengedhetetlen egyedi elkülönítés társasan élő fajok esetén befolyásolhatja az alanyok túlélését, ezért körültekintően kell alkalmazni. Ezek az eredmények arra sarkalltak, hogy áttekintsem a fogságban tartott házi verebekhez kapcsolódó szakirodalmat, amelynek során a mortalitásra és a tartási körülményekre – beleértve az egyedi elkülönítés módszereit – vonatkozó adatok meglepő hiányát tapasztaltam.

Értekezésem eredményeivel az elsők között bizonyítottam az innovatív viselkedés kapcsolatát a rátermettséggel, valamint a társas viselkedéssel. Ennek köszönhetően bepillantást nyerhetünk az egyedi innovativitásban tapasztalható variabilitás kialakulásának mechanizmusaiba is.

RESUMEN

Vivimos en un entorno altamente cambiante que compartirnos con otras especies y, por lo tanto, además de nuestra curiosidad innata por comprender los procesos naturales, también es nuestra responsabilidad buscar un mayor entendimiento de los mecanismos usados por otras especies para hacer frente a las perturbaciones humanas. La idea de que la cognición y la flexibilidad conductual permiten respuestas rápidas a las fluctuaciones ambientales y, por lo tanto, que pueden desempeñar un papel esencial en los procesos de adaptación de las especies se ha abordado en ecología del comportamiento durante las últimas décadas. En mi tesis, investigo la relación entre innovación y diferentes indicadores de éxito reproductivo, así como con el comportamiento social en dos especies de aves sinantrópicas.

En la primera parte de la tesis estudié la asociación entre innovación y diferentes medidas de éxito reproductivo en carboneros comunes (Parus major) de vida libre. Las parejas de carboneros, tanto en ambientes urbanos como forestales, que resolvieron una tarea de eliminación de obstáculos más rápido durante la reproducción tuvieron un mayor éxito de eclosión y un mayor número de volantones. Estos resultados sugieren un vínculo positivo entre innovación y eficacia biológica, aunque esta correlación no se detectó en otra tarea de extracción de alimentos. Además, la habilidad de las hembras en la misma tarea de eliminación de obstáculos estuvo relacionada positivamente con la tasa de crías de extra-pareja en la nidada. Sin embargo, la tasa pollos extra-pareja no estuvo relacionada con el éxito de resolución de problemas del padre social. Parejas de individuos altamente neofóbicas tuvieron menor probabilidad de tener pollos extra-pareja en sus nidadas que parejas menos neofóbicas. En conjunto, estos resultados sugieren que la innovación puede aumentar el éxito reproductivo y la promiscuidad en carboneros comunes.

En la segunda parte de mi tesis, usando bandadas de gorriones domésticos (Passer domesticus) en cautividad, demostré que, en contra de lo esperado, las aves no interactúan con otros individuos de la bandada de acuerdo a su aparente (manipulado experimentalmente) éxito de resolución de problemas, sino que lo hacen en base a la capacidad real de innovación. Los gorriones innatamente innovadores fueron atacados por otros individuos de la bandada con mayor frecuencia que los individuos menos innovadores, pero los gorriones no mostraron preferencia hacia individuos innovadores cuando acompañaban a sus congéneres. Esto sugiere que el robo agresivo de alimentos (una estrategia de alimentación frecuente en gorriones) por

parte de individuos innovadores es probablemente más importante que el beneficio obtenido del aprendizaje social a partir de individuos innovadores en la búsqueda de alimento.

En el mismo experimento, encontré que los gorriones sin ningún contacto visual otros conspecíficos durante los primeros días de cautiverio sufrían una alta mortalidad, lo que se aliviaba permitiendo el contacto visual con otros gorriones de forma intermitente. Esto sugiere que el aislamiento visual, que a menudo es necesario cuando se estudia innovación individual, podría aumentar la mortalidad en especies sociales y, por tanto, debe aplicarse con precaución. Motivado por estos hallazgos, realicé una revisión sistemática sobre la mortalidad de gorriones domésticos en cautiverio en la literatura científica y encontré que la mayoría de las publicaciones carecen de datos suficientes sobre la supervivencia y las condiciones de cautiverio, incluyendo los relacionados con los regímenes de aislamiento visual, de los individuos sujetos a estudio.

Estos resultados proporcionan las primeras evidencias de la conexión entre el comportamiento innovador, la eficacia biológica y el comportamiento social, arrojando luz sobre los mecanismos que moldean la variación individual en innovación dentro de una especie.

CHAPTER I.

GENERAL INTRODUCTION

1.1. Behavioural flexibility, innovation

Non-human animals face challenges posed daily by our anthropogenically modified world. Apart from the direct impacts of the "super predator" (Darimont et al. 2015), humans impose a striking array of effects on wildlife. Urbanization triggered habitat change, one of the largest scale anthropogenic alteration of the environment, has several effects on non-human animal (henceforth 'animal') populations and communities, for example by rapidly and extensively altering the structure of habitats and food availability (for non-avian animals reviewed by McKinney 2008; for birds by Seress and Liker 2015). Hundreds of millions of birds die each year due to collisions with man-made structures, it arguably is one of the main sources of anthropogenic mortality of birds in the United States of America (Smallwood 2013; Loss et al. 2014), and linear establishments such as roads with their traffic cause a tremendous negative effect on animal abundance (Fahrig and Rytwinski 2009). Altered food availability in urban habitats influences diet composition, which in turn affects not only individual condition, but also breeding performance (Harrison et al. 2010; Plummer et al. 2013). Moreover, direct anthropogenic effects go far beyond city limits; fisheries threat non-target marine species through incidental capture in a variety of fishing gear, causing human induced decline in some populations of these species, many of which are threatened (see e.g. the review for USA fisheries by Moore et al. 2009). Another risk for marine animals is to ingest or to entangle with debris of mainly land originated plastic waste (e.g. for marine turtles, see Schuyler et al. 2014). Furthermore, one of the most important phenomena of human influence on the Earth's ecosystem, the facilitation of the spreading of species outside their original range, has a detrimental effect on the native species in the way of their expansion, and requires adaptation from the invaders and the invaded alike (Clavero and García-Berthou 2005). These rapid processes that leave their marks even at the most remote corners of the biosphere have led to the introduction of a new era in the history of Earth, the so called "Anthropocene".

The profound changes in the environment caused by human activity are either distinct from the challenges animals met in their evolutionary past (e.g. habitat fragmentation caused by linear establishments), or come at a rate much faster than usual on an evolutionary time scale (e.g. large-scale habitat change caused by the combined effect of urbanization and climate change). Finding a way to cope with daily life in a swiftly changing world probably has never been more pressing for the individual animals. For humans, to mitigate the negative effects we have on wildlife it is imperative to understand the mechanisms by which animals may react to the alterations (Greggor et al. 2019). Three basic mechanisms may be implemented by organisms in order to counteract these effects and keep on surviving and reproducing: dispersion to habitats that are more favourable, genetic adaptation, and phenotypic plasticity. Dispersion is often inhibited by natural or anthropogenic barriers, and although evolutionary changes are always under way, the speed of genetic alterations may at times be unable to keep the pace with environmental changes, especially for species with relatively long generation time. However, the expression of a genotype can vary through phenotypic plasticity, allowing alternative phenotypes of a certain genotype to occur (West-Eberhard 1989), in order to adapt to environmental conditions. This type of adaptation may precede and complement micro-evolutionary processes (Miranda 2017), and can come in various forms. It may include, mutually non-exclusively and possibly non-independently, morphological variance (Repka and Pihlajamaa 1996), physiological changes (McKechnie et al. 2006), or behavioural responses. Note that behavioural responses are particularly labile; therefore, it might be especially appropriate for giving prompt responses to environmental challenges. Behaviour itself is partially genetically determined, the extent of which varies with species and trait (Yong-Kyu 2009). Heritability of behaviour normally ensures that species cope well with the dominant abiotic and biotic interactions that naturally occur in their native habitat. However, if these conditions change, existing behavioural patterns might prove inappropriate, indeed they may induce negative effects on individual fitness. Behavioural flexibility, which is the ability of an individual to change its existing behavioural patterns (West-Eberhard 1989), can enhance the adjustment of behaviour to the new conditions. For example, bird species with more flexible behaviour are more successful invaders, and in temperate Palearctic birds higher behavioural flexibility, larger brain size, and higher propensity for novel behaviours help resident species to cope with seasonal changes (Sol et al. 2002, 2005). This is furthered by the advantage that behavioural flexibility also allows for reversibility when fluctuation of stimuli necessitate it (Van Buskirk 2012); for example abandoning hiding behaviour after predators became absent results in more effective foraging (Orizaola et al. 2012). Still, in case of some anthropogenic changes behavioural plasticity might prove maladaptive, and therefore can further the negative impacts on a population contributing to the operation of ecological traps (López-Sepulcre and Kokko 2012); for example failed breeding of caddis fly *Hydropsyche pellucidula* on glass buildings (Kriska et al. 2008), or attempted breeding of common terns (*Sterna hirundo*) on rod fishing platforms that failed due to unpredictable human activity (personal observation).

For humans, innovations are key features in the history of the success of the species, and form the ultimate base of our culture. Similarly, innovation is prominent in the animal kingdom (Reader and Laland 2003) affecting ecological and evolutionary processes. Research on human innovation has an extensive literature, with the somewhat shorter history of works on animal innovation that roots back to the landmark paper of Fisher and Hinde (1949). Despite this prevalence of the topic, the definition of innovation remains controversial (Ramsey et al. 2007; Reader et al. 2016), although a demand for clarification of the term aroused decades ago (Kummer and Goodall 1985). Some authors regard innovation as a product, whereas others as a process (reviewed in Chapter I. of Reader and Laland 2003). Nevertheless, innovations are regarded as new behaviour patterns or modifications of existing behaviours in an unusual context to help an individual to utilize its environment in a novel way (Reader and Laland 2003; Griffin and Guez 2014, 2016; Tebbich et al. 2016). Innovation and flexibility of behaviour are traditionally regarded as related, where innovativeness is a component of behavioural flexibility and it is also a promising candidate as a proxy for it (Reader and Laland 2003; Reader et al. 2016). Behavioural flexibility and innovation however are not interchangeable concepts, as former is used for a broader domain of plasticity in behaviour (Audet and Lefebvre 2017), moreover recent studies suggest that the relationship between flexibility and innovative behaviour may vary; they may be positively or negatively associated or the link between them may be indirect (Reader and Laland 2003; Griffin et al. 2013a; Chow et al. 2016). Furthermore, Reader and Laland (2003) argue that innovations have the distinct property of being novel behaviours that are new not only for the individual itself, but also for the whole population, whereas flexibility may arise from the reaction norm of the species. The significance of innovative behaviour is conspicuous, as a tendency to innovate appeared independently in different taxa, meanwhile convergent evolutionary processes linked to innovation are described even in phylogenetically less related taxa (e.g. selection towards larger brain size, see Lefebvre et al. 2004; Overington et al. 2009b; Reader et al. 2011).

Innovative behaviours have become a central topic in the past decade, given their vast potential to facilitate adaptation to novel or changing environments (Griffin and Guez 2014; Reader et al. 2016). Innovation on one hand can bring benefits, and believed to be adaptive by enabling animals to better exploit their environment; e.g. find novel food resources (Fisher and Hinde 1949), use novel materials to repel parasites (Suárez-Rodríguez et al. 2013), attain more attractive sexual displays (Elias et al. 2006; Madden 2007), or deceive social companions in order to acquire resources (Byrne 2003). On the other hand, innovative behaviour is expected to have costs; besides the time and energy invested in such behaviour it is assumed for example to increase predation risk (Overington et al. 2011b), and it may incur risk of injury or poisoning (Bostic and Banks 1966), or elevated parasite load (Garamszegi et al. 2007; Vas et al. 2011). The trade-off between these fitness costs and benefits should determine the occurrence of innovation, yet studies investigating them are still scarce.

1.2. Measuring innovation and understanding its underlying processes

To assess innovativeness, two distinct approaches are used in animal behaviour research (Griffin 2016; Reader et al. 2016). Both approaches can be used to obtain measures to test ecological and life history correlates, and both have their advantages and their pitfalls. Firstly, innovativeness of different taxa may be evaluated by counting the observations of spontaneous innovations recorded in the scientific literature for each taxon ("innovation counts"). These may reflect natural innovation rates, and are suitable for carrying out large scale comparative studies (Overington et al. 2009b; Reader et al. 2011; Navarrete et al. 2016; Sol et al. 2016). On the other hand, such studies tend to have coarse resolution, and are likely to be biased (e.g. innovations seemingly unimportant for the observers may remain unreported). Furthermore, such studies require the data of extensive fieldwork for each species. Secondly, for measuring the innovativeness of individuals, researchers may develop various assays creating situations where individuals are given the opportunity to innovate in pre-defined tasks ("innovative problem-solving"; widely used examples are extractive foraging tasks). Such studies enable repeated and thorough investigation of processes such as social transmission and manipulation of possibly influential factors. However, the relevance to naturally occurring innovations, the authenticity of motivation, the fairness to motor- and perceptual capabilities of the study species might be questioned in these cases. Nevertheless, it seems that these issues can be addressed properly, and both approaches detect similar underlying processes of innovative behaviour, therefore both "innovation counts" and "innovative problem-solving" assays are reliable measures of innovativeness (Griffin and Guez 2014; Reader et al. 2016).

Studying animal innovations in either way is appealing also because it may offer a way to understand the ecological significance of cognitive skills by which the information from the environment is acquired, processed, stored, and acted upon (Shettleworth 2010). Innovativeness has been proposed to be an emergent trait, arising from a combination of several individual characteristics shaped by environmental variability (Griffin 2016; Sol et al. 2016). Innovativeness has been hypothesized to be facilitated by personality traits like novelty-seeking tendencies (such as exploration and neophilia, Greenberg 2003), persistence in trials (Guez and Griffin 2016), by non-cognitive mechanisms such as motor diversity (Griffin et al. 2014), and by cognitive abilities such as efficiency at operant learning (Overington et al. 2011a; Griffin et al. 2013a). Griffin and Guez (2014) reviewed the growing empirical evidence and concluded that the three most consistent predictors of problem-solving performance were learning speed, motor skill diversity, and persistence. Although the empirical studies of problem-solving performance provided controversial evidence on the effect of some cognitive and personality traits (Griffin et al. 2013a; and reviews by Griffin and Guez 2014, 2016), these traits might still be important components of innovations in nature. Exploration for example increases the likelihood of encountering and engaging in novel situations (Tebbich et al. 2016), while learning and memory help to maintain the new behaviours in the individual's repertoire and spread these in the population (Reader and Laland 2003; Tebbich et al. 2016). Recent evidence suggests for instance that simple feeding innovations (e.g. feeding on a previously unused plant species) are not correlated with brain size, but technical innovations (e.g. using a thorn as a lever to skin the prey) are more frequent in taxa with larger brain size (Overington et al. 2009b; Navarrete et al. 2016). Recently, a candidate neuronal mechanism was proposed by Audet et al. (2018) for evolution to act upon in the selection of innovativeness. Post-synaptic density of a receptor promoting neuronal plasticity (i.e. learning) was higher in the more innovative Barbados bullfinch (*Loxigilla barbadensis*) compared to the closely related but less innovative black-faced grassquit (*Tiaris bicolor*), a mechanism that seems to be conservative across different taxa (Tang et al. 1999). While innovative problem-solving performance does not necessarily reflect cognitive capacity (Rowe and Healy 2014; Thornton et al. 2014), several cognitive processes have been suggested to be associated with animal innovations. For example, empirical work on mechanisms of problem solving has implicated operant conditioning (Overington et al. 2011a) and inhibitory control (Thornton and Samson 2012), whereas other studies have discussed the potential role of insight (Bird and Emery 2009) and classifying the encountered stimulus as novel (Greggor et al. 2015). Therefore, problem-solving ability has been put forward as a candidate cognitive trait (Morand-Ferron et al. 2015).

1.3. Innovation and reproduction

Although the prevalence and potential advantages of innovation is discussed widely by behavioural ecologists, its fitness consequences are surprisingly neglected by empirical studies. However, in recent literature there has been an increasing interest in assessing the strength of selection on cognitive traits in the wild (Rowe and Healy 2014; Morand-Ferron and Quinn 2015), and evidence is accumulating that innovative behaviour can increase fitness through mate choice and parental care. For example, better problem-solving performance is associated with higher mating success in male satin bowerbirds (*Ptilonorhynchus violaceus*, Keagy et al. 2011), with plumage traits attractive in mate choice in male siskin (*Carduelis spinus*, Mateos-Gonzalez et al. 2011), and with larger brood size and higher nestling survival in great tits (Cauchard et al. 2013). Note however that the correlation between innovativeness and specific components of fitness varies between species (Keagy et al. 2011; Isden et al. 2013), between populations of the same species (Cole et al. 2012; Cauchard et al. 2013), and among different components of fitness in the same population (Cole et al. 2012). The reasons for this heterogeneity are not yet fully investigated.

Innovativeness is thought to co-evolve with life-history traits as part of a general strategy to cope with environmental changes (Sol et al. 2016). Variation in innovativeness has significant implications for ecology and evolution; for example, within various species, individuals living in harsh, high-elevation environments (reviewed by Pravosudov and Roth 2013), and in urbanized habitats (Sol et al. 2011; Papp et al. 2015; Ducatez et al. 2017) were found to have better problem-solving performance compared to conspecifics living at low elevations and in non-urbanized habitats, respectively. This may be because innovativeness can enhance breeding success (Cole et al. 2012; Cauchard et al. 2013) or survival during harsh winters (Kozlovsky et al. 2015), for example, by increasing foraging efficiency (Cole et al. 2012; Kozlovsky et al. 2015). Although according to these findings one may expect that fitness consequences of innovativeness vary among habitats, such that innovativeness is more favoured in more challenging environments, there were no empirical studies to address this assumption before my PhD work.

Innovativeness can not only be beneficial for the individual itself but also to its mate, so it may play a role in mate choice (reviewed by Boogert et al. 2011). An innovative mate may provide direct benefits; for example, birds that incorporate cigarette butts into their nest material suffer from fewer ectoparasites in their nests (Suárez-Rodríguez et al. 2013; but see Suárez-

Rodríguez and Garcia 2014). If innovativeness is heritable, an innovative mate can also provide "good genes" for the offspring; for example, this might explain why male satin bowerbirds with better problem-solving performance have higher mating success despite providing no direct benefit to females (Keagy et al. 2011). Candidate components of innovativeness, such as general intelligence in humans and exploratory behaviour in great tits, have also been shown to be heritable (Dingemanse et al. 2002; Deary et al. 2009) and important in mate choice (van Oers et al. 2008; Prokosch et al. 2009; Patrick et al. 2012), although Quinn et al. (2016) found low heritability for problem-solving success in great tits. Thus, further empirical studies are needed to clarify the role of innovativeness in breeding behaviour and reproductive success.

Along these lines, the appealing notion that innovativeness may also play a role in extra-pair sexual behaviour has received little or no attention. Extra-pair mating is a relatively common alternative reproductive tactic in pair-bonding birds that influences fitness (Griffith et al. 2002); it is obviously beneficial for the fertilizing males by increasing the number of their offspring, whereas for females the advantages of such behaviour are not so straightforward. The potential benefits for females include a possible increase in genetic diversity of their broods, or the acquisition of "good genes" for their extra-pair offspring if their extra-pair mates have superior qualities relative to their social mate (Charmantier et al. 2004). According to these, females could benefit from extra-pair matings, especially with males that are more innovative than their social mates are. Alternatively, innovativeness may not be causally linked to the propensity to engage in extra-pair behaviour, but it may allow for it through time management trade-off between such behaviour and other activities like foraging or territorial behaviour. For example, if innovative individuals are more efficient foragers collecting their food more quickly, they may seek extra-pair partners in their spare time (Westneat and Stewart 2003; Cole et al. 2012). An apparent relationship between innovativeness and promiscuity however might be due to a link with independent trait(s) associated to both, such as personality. Innovativeness and promiscuity have been found to be positively linked with novelty seeking, and exploratory behaviour, respectively (Patrick et al. 2012; Bókony et al. 2014). Despite the widespread phenomenon of extra-pair sexual behaviour (Griffith et al. 2002) and the growing interest in innovativeness' role in reproductive success, to my knowledge before my PhD work there were no empirical studies scrutinizing the relationship between infidelity and innovativeness.

1.4. Innovation and social interactions

In group-living species, innovative behaviours may have fitness consequences not only for the innovative individuals but also for their group-mates, thus innovativeness may shape social relationships. For example, in foraging groups innovative members can make novel food sources available for their group-mates in various ways (Liker and Bókony 2009; Morand-Ferron and Quinn 2011). First, group-members may obtain food discovered by innovators either by food sharing or non-aggressive scrounging (Giraldeau and Caraco 2000; Boogert et al. 2010), or by aggressively exploiting the innovator's efforts e.g. via kleptoparasitism or aggressive scrounging (Lendvai et al. 2006; Iyengar 2008; Tóth et al. 2009a). Second, by observing the innovator, group-members may copy and learn its behavioural techniques and thereby can exploit the new food sources on their own (Giraldeau et al. 1994; Altshuler and Nunn 2001). Social learning has long been suggested to explain the spread of some well-known foraging innovations like milk bottle opening by birds or potato washing by macaques (Fisher and Hinde 1949; Kawai 1965; Lefebvre 1995; Reader and Laland 2003). Recently such social transmission of innovation has been proved empirically; an experimentally introduced foraging innovation spread through detectable social network ties in a wild great tit population (Aplin et al. 2015). It is worth noting that the social environment may shape innovativeness; for instance, if innovators are frequently exploited through aggressive competition, the costs of innovative behaviour might exceed the benefits, which would lead to a decrease in the propensity to innovate.

Given the mechanisms above, the social relationships of group-members might be influenced by their innovativeness in various ways. First, if higher dominance rank facilitates the social exploitation of group-mates, e.g. through aggressive scrounging (Wiley 1991; Liker and Barta 2002), it may pay off for group-members to attain dominance over the innovators. For example, this can be achieved by more frequent or more intense aggression towards the most innovative group-mates than towards other group-mates. Second, if innovations can be learned or shared (Liker and Bókony 2009; Morand-Ferron and Quinn 2011; Ashton et al. 2019), it may be worth to maintain closer spatio-temporal associations with the innovators than with less skilled group-mates, because such associations may promote social learning as in the case of song and other sexual behaviours (Freeberg 1999; Poirier et al. 2004). Furthermore, if affiliative relationships enhance the efficiency of social learning and/or the probability of food sharing (reviewed by Stevens and Gilby 2004; and see de Kort et al. 2006), group-mates may increase affiliative behaviours and/or reduce aggression towards the innovators. So far, only correlative studies addressed these possible social consequences of innovativeness, producing mixed results. For example, dominance was positively (Boogert et al. 2008), or negatively (Cole and Quinn 2012) related to, or not related (Benson-Amram and Holekamp 2012) to problem-solving success in various species. Similarly, social associations may (Aplin et al. 2012) or may not (Boogert et al. 2008) predict the spread of novel behaviours. Despite the extensive research on animal innovation (Griffin 2016), and that some well-studied species live gregariously (Boogert et al. 2008), to my knowledge before my PhD work there were no experimental studies addressing the causal influence of innovativeness on aggressive and affiliative social behaviour.

CHAPTER II.

THESIS OBJECTIVES

Throughout my PhD studies that led to this thesis, my general aim was to better understand the links between innovative behaviour and different aspects of individual success in birds; in order to achieve this goal I used the great tit and the house sparrow as model species. In the studies presented here, first I measured the problem-solving success and breeding performance of free-living great tits to contribute to the understanding of the fitness consequences of innovativeness. Furthermore, in the same study system of great tits I investigated how innovativeness is related to extra-pair mating behaviour. To investigate whether individuals behave differently towards their innovative and less innovative conspecifics I manipulated individual innovativeness and measured social behaviour of captive house sparrows. Additionally, the study of captive house sparrows revealed an issue of housing conditions for social birds during problem-solving assays that I aimed to address more generally.

The studies included in this thesis were carried out as part of a project of the MTA-PE Evolutionary Ecology Research Group (formerly known as Ornithological Research Group) at the Department of Limnology, University of Pannonia. I participated in all phases of the work detailed in the following chapters, from planning of the studies to the writing of the publications. In this thesis, I investigated the following topics:

2.1. Problem-solving performance and breeding success of great tits in urban and forest habitats

Innovative behaviour might be more beneficial in challenging environments. According to this idea, I hypothesized that innovativeness is linked with reproductive success, and that selection favours this trait more strongly in urban than in non-urban habitats. Therefore in ***Chapter III***, I tested the predictions that (1) urban birds are more innovative than non-urban conspecifics, and that (2) superior problem-solvers have higher breeding success than birds with low problem-solving performance, and finally that (3) the latter difference is larger in urban than in non-urban habitats. To test these predictions I measured problem-solving performance in two tasks while monitoring breeding success in free-living great tit populations in two urban and two non-urban habitats.

2.2. Problem-solving performance and promiscuity in great tits

If innovativeness is linked to fitness, it might play a role in mate-choice and extra-pair sexual behaviour, therefore I hypothesized that innovativeness is associated with promiscuity. In ***Chapter IV***, I tested whether male and female problem-solving performance is correlated with the occurrence and number of extra-pair offspring in their broods. To investigate this relationship I used the same study system of free-living great tits as in ***Chapter III***.

2.3. Problem-solving success and its social consequences in house sparrows

In gregarious species, individual innovativeness might benefit not only the innovator, but also the group mates. Thus, I hypothesized that innovativeness of the individuals is taken into account in their social relationships in two alternative ways. Firstly, if higher rank in group hierarchy promotes the exploitation of innovators, the latter individuals would suffer more aggressive interactions from group mates. Secondly, if innovation is beneficial to group-mates because it can be learned from innovators, then group-mates are expected to maintain closer spatial associations with innovators than with non-innovative individuals. I tested these predictions in ***Chapter V*** by measuring individual innovativeness and manipulating apparent innovativeness of captive house sparrows, then recording aggressive interactions and spatial associations in small flocks.

2.4. Mortality of captive house sparrows

The last study is a follow-up of an unforeseen result of ***Chapter V***, in which I observed an unexpectedly high mortality among the house sparrows while studying their problem-solving performance. In ***Chapter VI***, I investigated the possible causes of the mortality, and motivated by my findings I carried out a systematic review of the literature on captive house sparrows to assess the mortality associated with the various housing conditions required for individual behavioural assays.

CHAPTER III.

INNOVATIVENESS AND REPRODUCTIVE SUCCESS

Abstract

Success in problem-solving, a form of innovativeness, can help animals exploit their environments, and recent research suggests that it may correlate with reproductive success. Innovativeness has been proposed to be especially beneficial in urbanized habitats, as suggested by superior problem-solving performance of urban individuals in some species. If there is stronger selection for innovativeness in cities than in natural habitats, we expect problem-solving performance to have a greater positive effect on fitness in more urbanized habitats. We tested this idea in great tits breeding at two urban sites and two forests by measuring their problem-solving performance in an obstacle-removal task and a food-acquisition task. Urban pairs were significantly faster problem-solvers in both tasks. Solving speed in the obstacle-removal task was positively correlated with hatching success and the number of fledglings, whereas performance in the food-acquisition task did not correlate with reproductive success. These relationships did not differ between urban and forest habitats. Neophobia, sensitivity to human disturbance, and risk taking in the presence of a predator did not explain the relationships of problem-solving performance either with habitat type or with reproductive success. Our results suggest that the benefit of innovativeness in terms of reproductive success is similar in urban and natural habitats, implying that problem-solving skills may be enhanced in urban populations by some other benefits (e.g. increased survival) or reduced costs (e.g. more opportunities to gain practice with challenging tasks).

This chapter is a modified version of the research article “Preiszner, B., Papp, S., Pipoly, I., Seress, G., Vincze, E., Liker, A. & Bókony, V. (2017) Problem-solving performance and reproductive success of great tits in urban and forest habitats. *Animal Cognition* 20:53-63.”

3.1. Introduction

Accumulating evidence suggest that innovative behaviour can have positive fitness consequences (Keagy et al. 2009; Mateos-Gonzalez et al. 2011; Cauchard et al. 2013), but these benefits may vary between habitat types, and selection may favour an innovative phenotype more strongly in more challenging environments. For example in chickadees (*Poecile spp.*) individuals living in harsher environments have enhanced spatial memory and better problem-solving performance compared to conspecifics living under milder conditions; this difference has been attributed to the importance of food caching, and the cognitive skills required for it, which is necessary for survival in harsh habitats (reviewed in Pravosudov and Roth 2013). Along a similar logic, innovativeness may be particularly important in urban environments, because urban animals are exposed to several kinds of novel or variable stimuli such as fragmented landscapes, noise and light pollution, disturbance by domestic animals and humans, and new food resources such as garbage (Sol et al. 2013). Accordingly, individuals from more urbanized habitats were found to be more successful in certain problem-solving tasks in three avian species (Liker and Bókony 2009; Sol et al. 2011; Audet et al. 2016), although the relationship between urbanization and innovativeness is equivocal (Papp et al. 2015; Audet et al. 2016). Consequently, if innovativeness is particularly relevant in urban habitats, we may expect that it has a stronger effect on fitness than in non-urbanized habitats.

We tested this idea in the great tit, which is one of the most common breeding birds in both urban areas and natural forests in Europe (Burfield and van Bommel 2004). We measured innovativeness in urbanized and forest-dwelling breeding pairs in two different problem-solving situations, an obstacle-removal task and a food-acquisition task, and monitored their breeding success. We investigated whether 1) urban pairs outperform their forest-dwelling conspecifics in the speed of problem-solving, 2) individuals with superior problem-solving performance have higher breeding success within their habitats, and 3) the relationship between problem-solving performance and breeding success is more pronounced in urban habitats than in forests. Furthermore, we examined whether any of the above relationships is mediated or confounded by differences in three behavioural traits that have been found to be related to problem-solving performance as well as to urbanization in several species: neophobia (Sol et al. 2011; Miranda et al. 2013; Cauchard et al. 2013), sensitivity to predation risk (Seress et al. 2011; Cole et al. 2012) and sensitivity to human disturbance (Cole et al. 2012; Vincze et al. 2016).

3.2. Methods

We tested 55 wild great tit pairs nesting in artificial nest boxes in 2 urban and 2 forest habitats in 2013. The urban study sites are located in Veszprém (47°05’17”N, 17°54’29”E) and Balatonfüred (46°57’30”N, 17°53’34”E), whereas the forest study sites are a downy oak (*Quercus pubescens*) and south European flowering ash (*Fraxinus ornus*) forest at Vilma-puszta (47°05’02”N, 17°52’01”E) and a beech (*Fagus sylvatica*) and hornbeam (*Carpinus betulus*) forest near Szentgál (47°06’39”N, 17°41’17”E) in Hungary.

Throughout the breeding season we checked the nest boxes twice a week and recorded the number of eggs and/or chicks at each visit. The experimental protocol began by catching one of the parents (excepting a few pairs where one or both parents had already been ringed) using a nest box trap when the chicks were 5-9 (mean ± SE = 6.18 ± 0.16) days old, considering the day of hatching of the first chick as day 1. Upon capture we ringed the birds with a unique combination of a metal ring and 3 plastic colour rings, and we recorded their age class (2nd calendar year or older) and sex, both based on plumage characteristics (Svensson 1992). Ringing one of the parents before the behavioural tests ensured that the sex of the parents could be recognized unambiguously during all observations, as it was not always possible to sex the birds by plumage from the videos (see below). We trapped only one parent before the tests to minimize stress and the risk of nest desertion. Between days 6-16 of chick age we conducted five behavioural tests at each nest as detailed below; then we trapped and ringed the other parent (if it had not been ringed earlier) following the last test, so that individuals could be identified in later breeding episodes. Because trapping might have affected the birds’ behaviour (Schlicht and Kempenaers 2015), the trapping status of each individual (i.e. trapped a few days before the tests or not) and each pair (i.e. one or no parent trapped a few days before the tests) was taken into account in the analyses (see below). At the age of 13-17 (mean ± SE = 15.07 ± 0.12) days, we ringed the chicks and measured their body mass and tarsus length.

3.2.1. Behavioural tests

First we assayed the parents’ neophobia between days 6-10 (mean ± SE = 7.98 ± 0.16) of chick age. After 30 minutes of baseline observation we fixed a small rubber ball with adhesive putty on the platform next to the entrance of the nest box (Figure III.1, panel C), and observed the nest box until both parents entered the nest, or for 30 minutes. We assessed the neophobia of each parent by measuring the latency to enter the nest box after the observer had placed the ball and left the vicinity of the nest.

The next two tests were designed to assay problem-solving performance. First, all pairs were tested in an obstacle-removal task between 7-11 (mean ± SE = 9.15 ± 0.15; mean difference between forest and urban pairs: 0.19 ± 0.31) days of chick age. Before the test, during a 30 minutes period of baseline observation, there was a ca. 3×7 cm grey feather fixed with adhesive putty on the platform near the entrance. The birds had been familiarized with this situation because we had put a similar feather near the entrance upon the start of egg laying, and replaced it with another feather at every nest check (whether or not it was removed by the birds between the successive nest checks) until the obstacle-removal test. In most cases these feathers had been removed by the birds between the successive nest checks, but we kept no record whether or when it happened. At the start of the test we blocked the entrance by fixing a similar grey feather in front of it using magnetic tape, and observed the nest box until one of the parents removed the feather and entered the nest, or for 30 minutes. To remove the feather, the bird had to grab it with the beak or a foot to pull it off (Figure III.1, panel D).

In the second problem-solving test, the parents were tested in a food-acquisition task between 8-13 (mean ± SE = 10.35 ± 0.19; mean difference between forest and urban pairs: 0.56 ± 0.37) days of chick age. During the 30 minutes of baseline observation before the test we provided the birds with 3 mealworms (*Tenebrio molitor* larvae) in a well on the platform near the entrance of the nest box. This situation was familiar for the birds because we provided 3 mealworms in the same well upon every nest check from the start of egg laying. At the start of the test we topped up the number of mealworms in the well to 3, and we covered the well by a transparent plastic lid that was fixed at its two ends by sticking small pieces of toothpicks into prepared holes. In order to reach the mealworms, the birds had to remove at least one toothpick and move the lid, or lift the lid off from the toothpicks by pulling it upwards (Figure III.1, panel E). We observed the nest box until one of the parents removed the lid and took out at least one mealworm, or for 30 minutes.

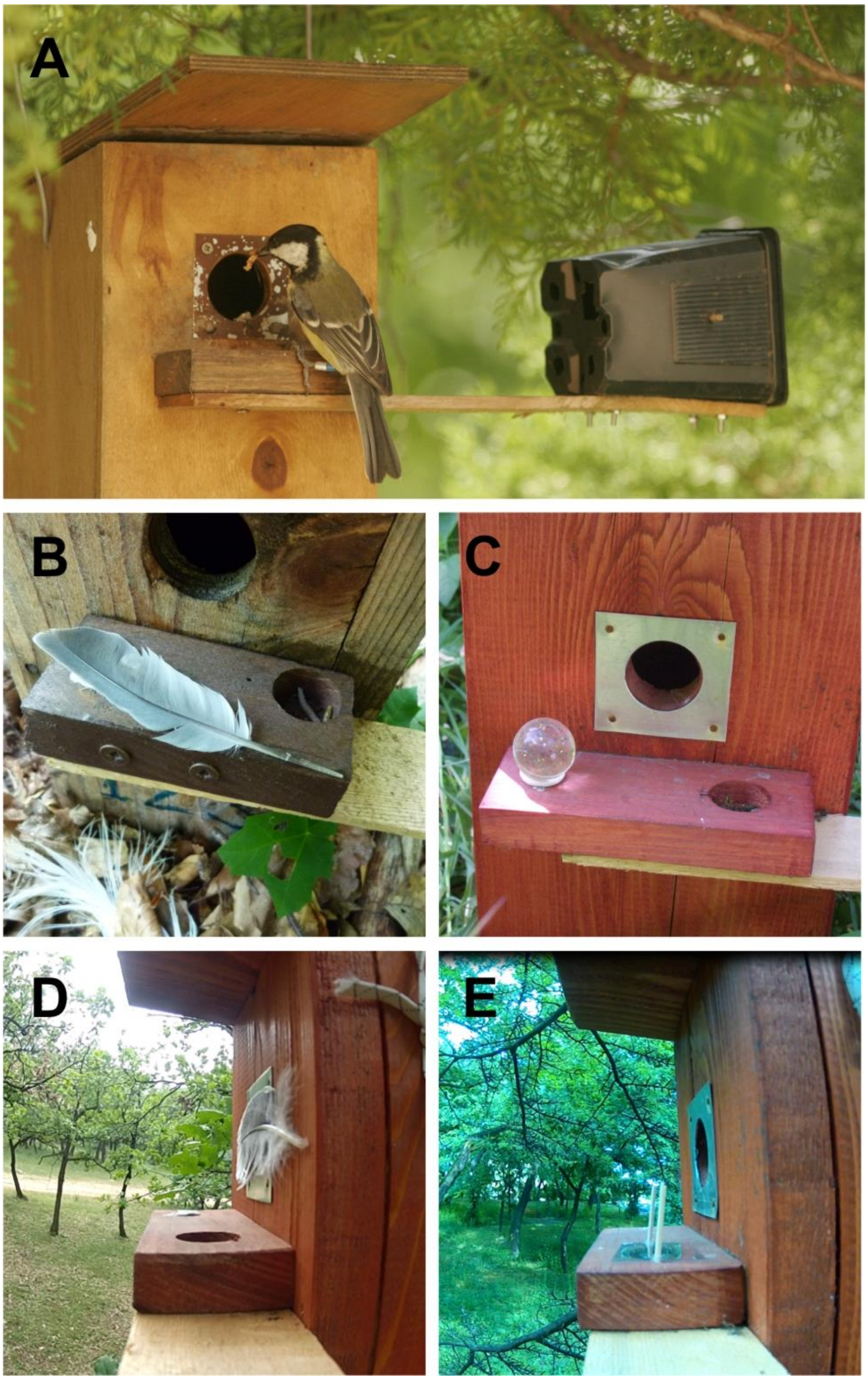

Figure III.1: Methods for observing problem-solving performance of breeding great tits.
A) Female at the nest box with a permanent hide for video camera.
B) Familiarizing the birds with the test equipment upon each nest check: feather fixed on the platform and mealworms placed in the well.
C) Rubber ball temporarily attached on the platform during the neophobia test.
D) Entrance blocked by a feather during the obstacle-removal task. For a video sample showing a solving bird, see: http://www.edge-cdn.net/video_1062366?playerskin=37016
E) Mealworms covered by a lid fixed with sticks during the food-acquisition task. For a video sample showing a solving bird, see: http://www.edge-cdn.net/video_1062368?playerskin=37016

After the first 3 tests, when the chicks were 9-16 (mean ± SE = 12.81 ± 0.14) days old, each pair was observed in two more behavioural assays, the order of which was randomly chosen at each nest. These two tests were designed to assess the birds' sensitivity to predation risk and to human disturbance. At the beginning of the predation-risk test we placed a ca. 1 m high tripod on the ground, setting up the top end 3 m from the nest box entrance. The observation started when the experimenter left the vicinity of the nest. After 15 minutes of baseline observation we fixed a taxidermally mounted Eurasian collared dove (*Streptopelia decaocto*) on the tripod for 10 minutes, then removed the dove and conducted an additional 10 minutes observation. After this, a taxidermally mounted Eurasian sparrowhawk (*Accipiter nisus*) was fixed on the tripod for 10 minutes, and after the removal of the sparrowhawk the observations were carried out for a further 10 minutes. Thus the entire test was 55 minutes long. We measured the number of visits (i.e. entering the nest box) per minute (henceforth visit rate) by both parents in each 10-minutes interval; then we quantified their response to predation risk as visit rate recorded in the 10 minutes after the removal of the sparrowhawk minus the visit rate recorded in the 10 minutes after the removal of the dove.

The human-disturbance test followed a similar design as the predation-risk test, but no tripod was placed near the nest. Again, the observation started when the experimenter left the vicinity of the nest. After the first 15-minutes baseline observation, a person stood under the nest box for 10 minutes. After the person had left, we observed the nest for a further 10 minutes, and thus the entire test was 35 minutes long. We measured the number of visits per minute by both parents in each interval; then we quantified their response to human disturbance as visit rate in the 10 minutes after the person had left minus the visit rate in the 15 minutes before the arrival of the person to the nest box.

Each test was conducted on a different day. All observations were made using a small (98 × 58 × 34 mm) camera hidden in a plastic box that was permanently attached to the nest box ca. 15 cm from the entrance (Figure III.1, panel A). All tests began with a few-minutes period that supposedly attracted the attention of the parent birds (i.e. the experimenter walked into their territory and installed the camera on the nest box and the other devices needed for the test); since the parents could hide in the canopy when approaching the nest boxes, it was not possible to ascertain when they became aware of the stimuli. The 5 behavioural tests were repeated with the same protocol in later breeding episodes in the same breeding season (2013) for a subset of the same pairs in order to test individual consistency in problem-solving performance.

3.2.2. Statistical analyses

In the problem-solving tests, we measured solving latency as the time the solving parent took to remove the feather in the obstacle-removal task or open the well in the food-acquisition task after it first landed at the entrance. We used the criterion of landing at the entrance because proximity to the task was necessary for starting to attempt to problem solve. Hence, time spent potentially visually inspecting the task at close range was included in the problem-solving latency. In contrast, during neophobia tests, birds typically entered the nest box very soon after landing. In this case, although birds occasionally spent considerable time inspecting the novel object form a greater distance, this time could not be quantified given our reliance on close-up video. If a bird landed on the nest box at least once during the 30 minutes of the test but did not solve, we considered it as a non-solver. Birds that did not visit the nest box during the 30 minutes of the test were treated as non-participating. Individuals whose mate solved the given task were treated as non-measured because their performance could not be quantified (i.e. the test ended when one of the parents solved, so it is unknown if the other parent would have been a solver, a non-solver, or non-participating if it had had 30 minutes). Non-measured and non-participating birds were excluded from all individual-level analyses (Table III.1). Non-solvers were assigned the maximal latency (1860 sec, i.e. the duration of the test plus 1 minute). To analyse whether problem-solving latency is individually consistent, we used the data of 26 pairs that were tested in 2 consecutive breeding episodes within the season. Within each task, we correlated the latencies between their first and second tests if the solver individual was the same in both tests or if none of the parents solved in one or both tests. In all other analyses (detailed below), we used only the data collected during the rearing of the first brood of the year for each pair.

To analyse the effects of habitat type and potential confounder variables on problem-solving performance, we used Cox's proportional hazards models with solving latency of the respective task as dependent variable, treating maximal latencies as censored observations. Initial models contained habitat type (urban vs. forest), provisioning rate (the number of visits of the parents during the baseline observation of the respective test divided by the number of nestlings alive on the day of the respective test), date of the test (number of days since 1st of May), age of nestlings on the day of the test, time of day at the start of the test (number of minutes since 7:00), and the parents' age class and trapping status (as explained below).

To measure breeding success, we calculated the following variables: clutch size (i.e. the maximum number of eggs observed in the nest); hatching success (i.e. the proportion of eggs that hatched); number of fledglings (i.e. number of nestlings alive at the age of ringing);

proportion of chicks fledged (i.e. the proportion of hatchlings that survived to ringing age); mean tarsus length (± 0.1 mm) and mean body mass (± 0.1 g) of fledglings measured at ringing. Linear mixed-effects models were used with study site as random factor to investigate whether each measure of breeding success is predicted by solving latency in the two problem-solving tasks. In the models of hatching success and proportion of chicks fledged, we used quasi-binomial error distribution with logit link function. Solving latency of the respective test, habitat type, hatching date of the first chick, parents' age class and trapping status (see below) were included in the initial models as predictors, along with the solving latency × habitat type interaction to test whether the effect of solving latency differs between urban and forest pairs.

In all analyses, we also tested the effects of neophobia, response to predation risk, response to human disturbance, and their interactions with habitat type by adding each to the initial models separately (we did not include all potential confounders into one model to avoid over-parametrization). Each initial model was then reduced by omitting the term associated with the largest p-value stepwise, except that we always retained the predictor that we were primarily interested in, i.e. habitat type in the Cox's analyses and problem-solving latency in the mixed models, regardless of their significance level, to estimate their effects even if they were not significant. Also, we always kept habitat type in the mixed models to control for the difference between urban and forest breeding parameters (Solonen 2001; Bailly et al. 2015). Other predictors and interactions were omitted if they had $p > 0.05$.

We used two approaches throughout the analyses: in one set we used pairs as the units of analysis while in the other set we used the data of individuals. This dual approach was necessary because we had only one solver individual per pair, so the confounding variables can be calculated in two equally relevant ways. First, when analysing pairs, we considered that breeding success may depend on the traits of both parents, thus we coded the parents' age class and trapping status as whether or not the pair contained at least one individual that was older than 2nd calendar year and had been trapped before the behavioural tests, respectively; and we expressed neophobia, response to predation risk, and response to human disturbance as the average of the two parents' values. Second, when analysing individuals, we focused on the traits of the solving parent (this could not be done in the analyses of pairs because there was no solving parent in the unsuccessful pairs). Thus, in the analyses of females, we compared the data of solver females to non-solver pairs (i.e. non-solver females) omitting those pairs in which the male was the solver because in these latter cases we could not measure female performance. Similarly, in the analyses of males, we used the data of solver males and non-solver pairs and omitted the pairs in which the female was the solver (note that this could not be done in the obstacle-removal task with reasonable power because there were only 5 successful males; thus this task was analysed only by using pair and female performance). In these individual-level analyses we used the solver parent's age class, trapping status, neophobia, response to predation risk, and response to human disturbance as predictors.

3.3. Results

3.3.1. Individual consistency of problem-solving performance

Individuals that were tested in two consecutive breeding episodes of the same year in the obstacle-removal task showed a strong correlation between the two repeated measurements (Spearman rank correlation, all birds: $r_s = 0.73$, $p < 0.001$, $n = 18$; females: $r_s = 0.72$, $p = 0.001$, $n = 17$; Figure III.2). Their solving time decreased from 13.36 ± 2.84 (median [IQR] = 7.10 [2.28 – 27.23]) minutes in the first test to 7.68 ± 2.91 (median [IQR] = 1.42 [0.53 – 4.98]) minutes in the second test (Figure III.2; paired t-test on the log(x+1) transformed data, all birds: $t_{17} = 4.87$, $p < 0.001$; females: $t_{16} = 4.50$, $p < 0.001$, solver females only: $t_{12} = 5.71$, $p < 0.001$).

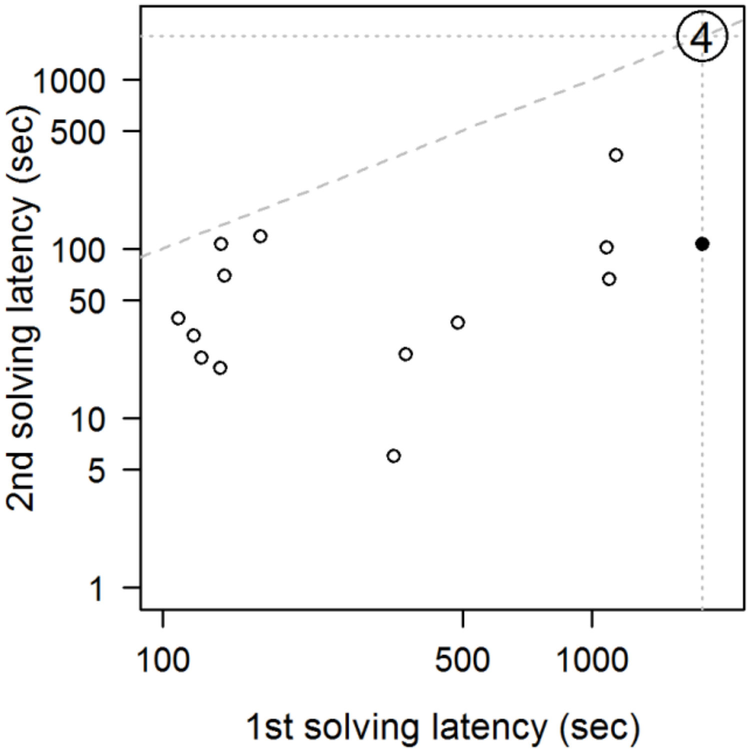

Figure III.2: Solving latency in the obstacle-removal task in two consecutive breeding episodes within one season. Solver females and males, respectively, are shown by empty and filled symbols; "4" notes 4 pairs that were unsuccessful in both tests. The dotted lines mark the maximal latency values (1800 sec); the dashed line indicates equality of latencies in the two tests. Both axes are on logarithmic scale.

Table III.1: Number of solver, non-solver, non-measured, and non-participating birds in two types of habitat in the two problem-solving tasks (the first test per task of each pair).

	Forest habitat				Urban habitat					
	Solver	Non-solver[a]	Non-measured[b]	Non-participating[c]	Solver	Non-solver	Non-measured	Non-participating	χ^2	p
Obstacle-removal task										
Pairs (*n* = 52)	11	12	0	0	22	7	0	0	4.35	0.037
Males (*n* = 23)	2	11	9	1	3	7	19	0	0.71	0.400
Females (*n* = 46)	9	12	2	0	19	6	3	1	5.26	0.022
Food-acquisition task										
Pairs (*n* = 48)	7	14	0	0	18	9	0	0	5.26	0.022
Males (*n* = 34)	5	13	2	1	7	9	11	0	0.95	0.331
Females (*n* = 36)	2	14	5	0	11	9	7	0	6.96	0.008

The χ^2 and P values stand for χ^2 tests comparing the proportion of solvers and non-solvers between habitats.

[a] birds that landed on the nest box at least once during the 30 minutes of the test but did not solve

[b] individuals whose mate solved the given task were treated as non-measured because their performance could not be quantified

[c] birds that did not visit the nest box during the 30 minutes of the test

In the food-acquisition task, 10 out of 14 pairs were unsuccessful in both the first and the second test; one female was successful in the first but not the second test while one male and two females solved both tests within 2 minutes (Fisher's test for the 2 × 2 contingency table of the occurrence of success in the first and second food-acquisition test: p = 0.011). Solving latency did not correlate between the obstacle-removal task and the food-acquisition task (all birds: $r_s = -0.15$, p = 0.345, n = 43; females: $r_s = -0.29$, p = 0.155, n = 25; males: $r_s = 0.29$, p = 0.264, n = 18).

3.3.2. Urbanization and problem-solving performance

When tested for the first time in each task, urban pairs solved both tasks significantly more often (Table III.1) and faster than forest-dwelling pairs (Table III.2, Figure III.3). When we analysed the sexes separately, females showed the same habitat difference in both tasks while there was no difference between urban and forest males in either task (Table III.2; note that sample sizes were smaller for males than females in both tests, and effect sizes were similar for the sexes in the obstacle-removal task). No other investigated variable had statistically significant effect on solving latency in either task (for results of neophobia, response to predation risk, and response to human disturbance see Table S.III.1).

Table III.2: Effects of habitat urbanization and other traits on problem-solving latencies.

Model	Predictors	$b \pm$ SE	Z	p	e^b [95% CI]
Obstacle-removal task					
Pairs (*n* = 52)	Habitat[a]	1.27 ± 0.41	3.12	0.002	3.55 [1.60; 7.85]
	Provisioning rate[b]	-0.91 ± 0.37	-2.43	0.015	0.40 [0.19; 0.84]
Females (*n* = 46)	Habitat	0.95 ± 0.41	2.33	0.020	2.58 [1.16; 5.73]
Males (*n* = 23)	Habitat	0.69 ± 0.91	0.76	0.448	2.00 [0.33; 11.98]
Food-acquisition task					
Pairs (*n* = 48)	Habitat	0.90 ± 0.45	2.01	0.044	2.46 [1.02; 5.92]
Females (*n* = 36)	Habitat	1.78 ± 0.77	2.31	0.021	5.95 [1.31; 26.94]
Males (*n* = 34)	Habitat	0.48 ± 0.59	0.82	0.411	1.62 [0.51; 5.11]

Table shows the results of the final Cox's proportional hazards models. Positive parameter estimates (*b*) indicate positive effect on solving speed (i.e. shorter latencies). Exponentially transformed parameter estimates (e^b) show the proportional change of hazard ratio in response to unit change of predictors.

[a] urban compared to forest

[b] sum of visits of both parents in the 30-min pre-test observation, divided by the number of chicks

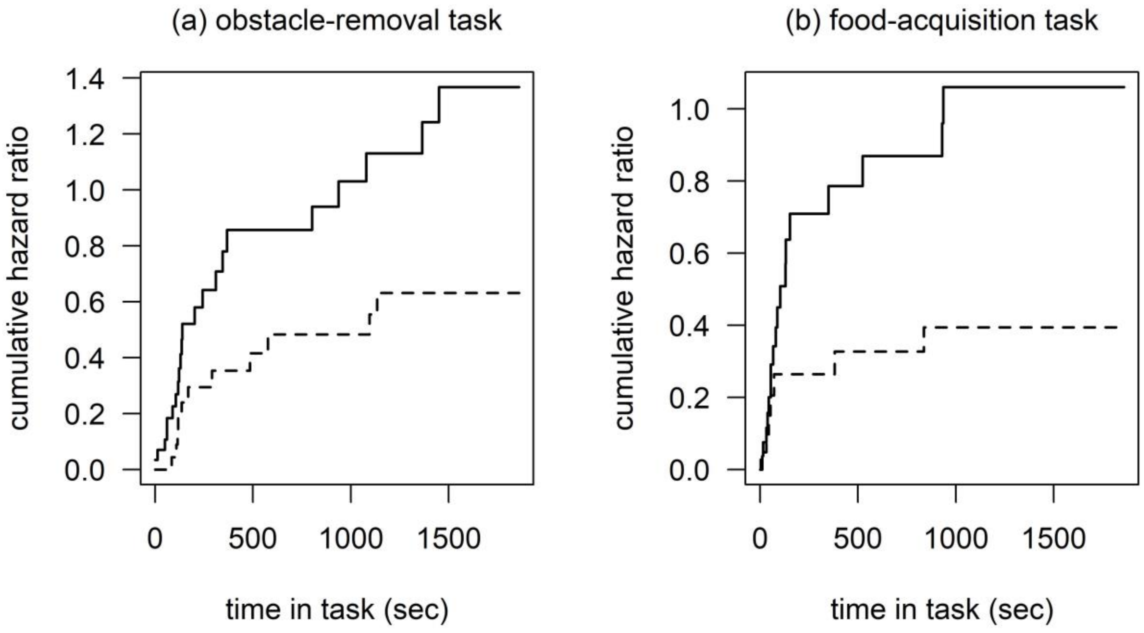

Figure III.3: Problem-solving latency in the two tasks in forests (dashed line) and urban habitats (solid line). The figures show the change over test time in the cumulative hazard ratio; a steeper increase in hazard ratio indicates faster problem-solving.

3.3.3. Breeding success and problem-solving performance

In the obstacle-removal task (Table III.3), faster pairs had higher hatching success (Figure III.4b) and more fledglings (Figure III.4c), but clutch size (Figure III.4a), proportion of chicks fledged (Figure III.4d), and fledglings' mean body mass or tarsus length (Figure III.4e-f) did not correlate with problem-solving latency. Clutch size, the number of fledglings, and mean fledgling mass were lower in urban than forest habitats (Table III.3). The interaction between solving latency and habitat type was not significant in any analysis (Table S.III.2). None of the variables describing breeding success was related to neophobia, response to predation risk, or response to human disturbance (Table S.III.3), and their interactions with habitat type in the 52 pairs that had valid data for the obstacle-removal test. All these results were qualitatively the same when we analysed females instead of pairs.

In the food-acquisition task, solving latency was not related to any measure of breeding success (Table S.III.4, Figure III.5) regardless the unit of the analysis (pairs, males, or females), and the interaction between solving latency and habitat type was also not significant in any analysis (Table S.III.5). None of the variables describing breeding success was related to neophobia, response to predation risk, or response to human disturbance (Table S.III.6), and their interactions with habitat type in the 48 pairs that had valid data for the food-acquisition test.

Table III.3: Effects of habitat urbanization and problem-solving latency in the obstacle-removal task on breeding success (*n* = 52 pairs).

Dependent variable	Predictors	*b* ± SE	*df*	*t*	*p*
Clutch size	Intercept	12.32 ± 0.40	47	30.83	<0.001
	Latency[a]	-0.02 ± 0.01	47	-1.13	0.265
	Habitat[b]	-3.15 ± 0.39	2	-8.08	0.015
Hatching success	Intercept	3.78 ± 0.57	47	6.61	<0.001
	Latency	-0.04 ± 0.02	47	-2.14	0.038
	Habitat	-0.95 ± 0.48	2	-1.98	0.187
Number of fledglings	Intercept	12.26 ± 0.67	47	18.36	0.000
	Latency	-0.05 ± 0.02	47	-2.45	0.018
	Habitat	-4.87 ± 0.76	2	-6.45	0.023
Proportion of chicks fledged	Intercept	5.97 ± 1.46	47	4.08	<0.001
	Latency	-0.02 ± 0.02	47	-0.97	0.336
	Habitat	-3.95 ± 1.43	2	-2.77	0.110
Fledgling body mass	Intercept	18.35 ± 0.81	45	22.58	<0.001
	Latency	-0.01 ± 0.02	45	-0.50	0.622
	Habitat	-3.37 ± 0.47	2	-7.10	0.019
	Hatching date[c]	0.11 ± 0.03	45	4.25	<0.001
	Trapping status[d]	-1.70 ± 0.57	45	-2.98	0.005
Fledgling tarsus length	Intercept	20.09 ± 0.29	45	70.04	<0.001
	Latency	0.01 ± 0.01	45	1.07	0.290
	Habitat	-0.70 ± 0.19	2	-3.63	0.068
	Hatching date	0.02 ± 0.01	45	2.63	0.012
	Trapping status	-0.58 ± 0.19	45	-3.00	0.004

The table shows the results of final mixed models (with study site as random factor; quasi-binomial error for hatching success and proportion of chicks fledged).

[a] problem-solving latency in minutes

[b] urban compared to forest

[c] number of days since 1st of May

[d] at least one vs. none of the parents trapped

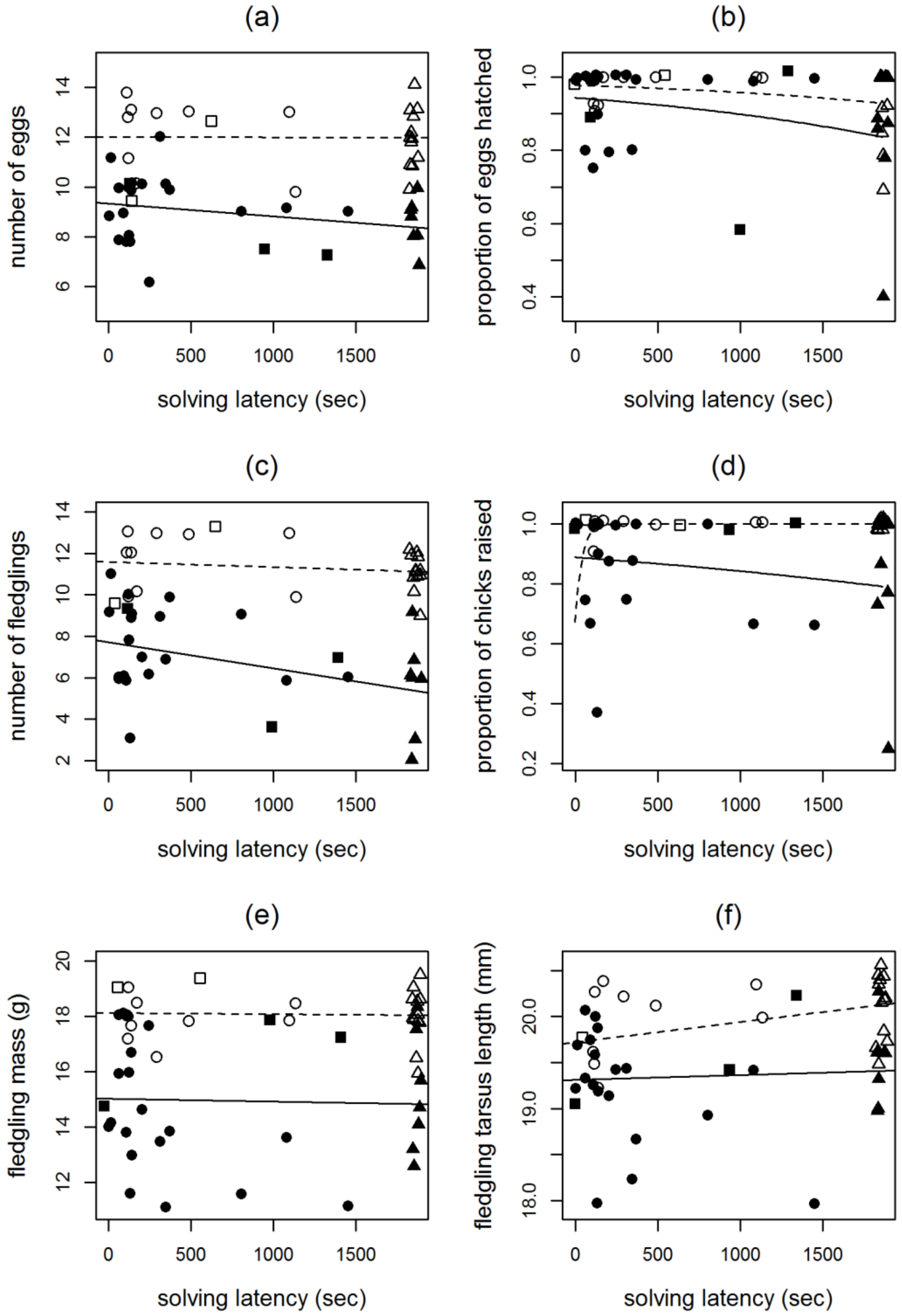

Figure III.4: Relationship of breeding success with solving latency in the obstacle-removal task in forests (dashed lines, open symbols) and urban habitats (solid lines, filled symbols). The lines were fitted from linear mixed models containing the interaction between habitat and solving latency. Circles, squares, and triangles denote pairs in which the solver was the female, the male, or none of the parents, respectively; overlapping data points were jittered.

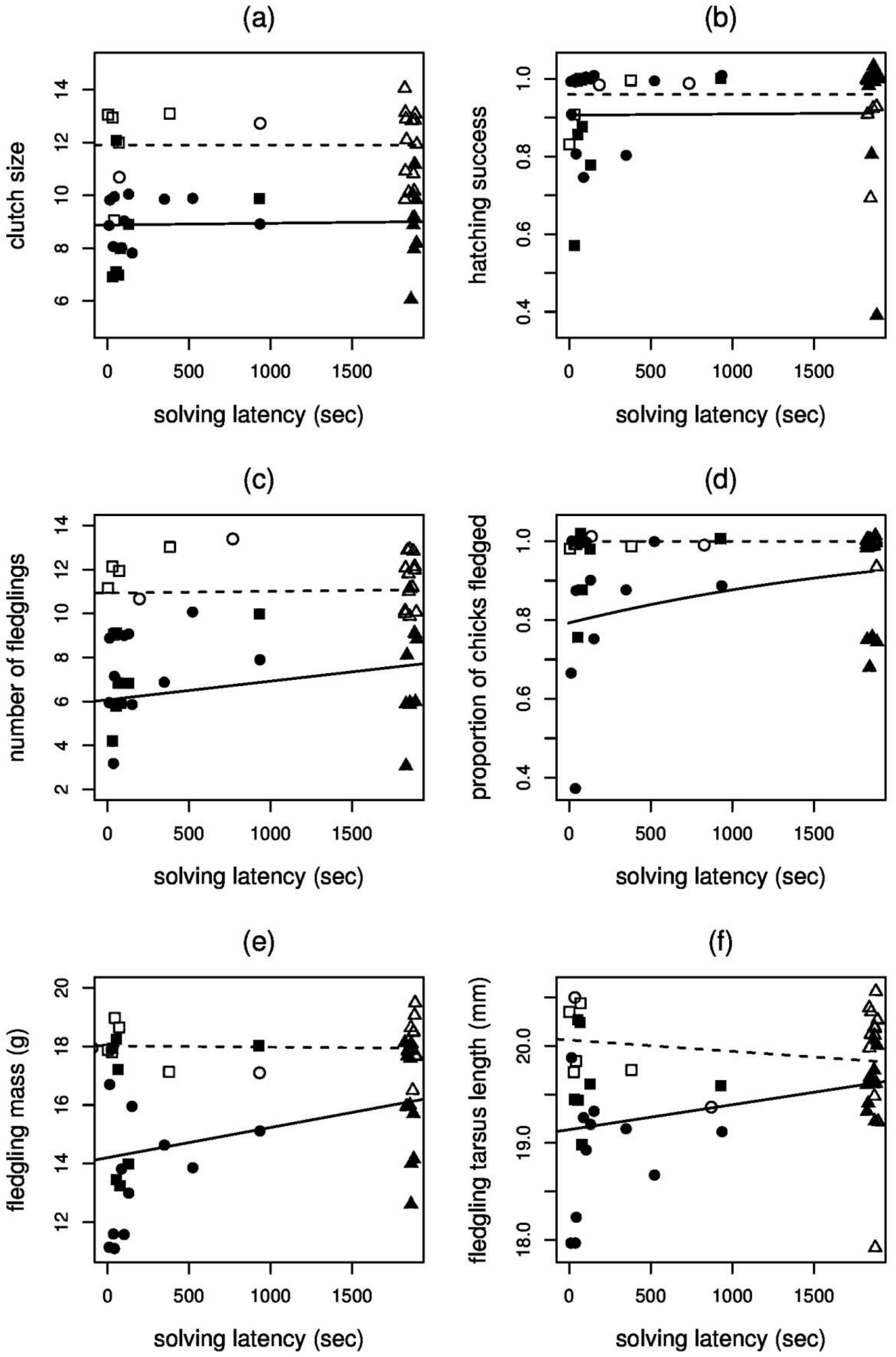

Figure III.5: Relationship of breeding success with solving latency in the food-acquisition task in forests (dashed lines, open symbols) and urban habitats (solid lines, filled symbols). The lines were fitted from linear mixed models containing the interaction between habitat and solving latency. Circles, squares, and triangles denote pairs in which the solver was the female, the male, or none of the parents, respectively; overlapping data points were jittered.

3.4. Discussion

In this study, we tested the innovative problem-solving performance of urban and forest-dwelling great tits in two tasks. In both tasks, we found that pairs in urban habitats were more successful (i.e. had lower latencies to solve, and higher proportion of solving) than pairs breeding in forests. Similar differences were found in food-extracting tasks in common mynas (*Acridotheres tristis*, Sol et al. 2011), Barbados bullfinches (Audet et al. 2016), and house sparrows (Liker and Bókony 2009), although the habitat effect seems to vary with task type and/or difficulty (Papp et al. 2015; Audet et al. 2016). In our present study, the habitat difference was significant in females but not in males. One possible explanation for this is that the tasks may have been more motivating for females than for males, because the reward in both situations was related to parental care, i.e. the access to the chicks in the obstacle-removal task and access to chick food in the food-acquisition task. Although urbanization may select for better problem-solving skills in birds, males may be less motivated to use those skills in a parental-care context because their confidence of paternity can be lower due to extra-pair matings. On average, ca. one third of the broods in great tit populations have been found to contain extra-pair offspring (reviewed by García-Navas et al. 2015), and female promiscuity occurs at all 4 of our study sites (***Chapter IV***, and Pipoly et al. 2019). Alternatively, the sex difference we found might be attributable to the lower statistical power for males due to smaller sample sizes, at least in the obstacle-removal test in which the estimated size of habitat effect was similar for the two sexes.

When looking at the relationships between problem-solving latencies and aspects of breeding success, we found no correlation with performance in the food-acquisition task, whereas performance in the obstacle-removal task correlated positively with hatching success and the number of fledglings, but not with the proportion of chicks that fledged or fledgling size. These results partially mirror and confirm further the findings of two similar studies on great tits in forest habitats (Cole et al. 2012; Cauchard et al. 2013). Measuring problem-solving performance in a lever-pulling foraging task prior to breeding, Cole et al. (2012) found that solver females had larger clutch sizes and more but not heavier fledglings than non-solver females, while the effect of male performance was much weaker. Cole et al. (2012) interpreted these findings as a result of solvers' more efficient foraging during the early stages of breeding when food is not yet abundant. Solvers had shorter working days and smaller foraging ranges which may have allowed them to invest more time to nest attendance (Cole et al. 2012). This may also explain the higher hatching success of solver females in our study. In another population, Cauchard et al. (2013) measured great tits' performance in a string-pulling obstacle-removal task during breeding and found that pair performance positively correlated with clutch size, hatching success and also nestling survival. This difference between populations might be due to fine-scale variation along environmental gradients in the pay-offs of problem-solving skills (Morand-Ferron et al. 2015).

Despite their superior problem-solving performance, urban pairs had significantly reduced breeding success compared to forest pairs in terms of clutch size and the number and weight of fledglings. These results are in line with findings on several avian species, indicating that urban birds face difficulties with obtaining the resources for egg production and chick feeding (Chamberlain et al. 2009; Seress et al. 2012; Bailly et al. 2015; de Satgé et al. 2019). We expected that, given such difficult conditions, superior problem-solving skills would confer disproportionately greater benefits to urban birds during reproduction than to forest birds. Surprisingly, however, we found no interaction between the effects of habitat type and problem-solving performance in either of our tests for any measure of breeding success. This was not due to any confounding effect of the birds' neophobia and sensitivity to predation risk or human disturbance, because none of these traits was correlated with either problem-solving performance or any measure of breeding success. Thus, our study revealed no strong difference between forests and urban habitats in the relationship between problem-solving and breeding success, providing no support for the idea that urbanization selects for enhanced innovativeness. A potential explanation is that increased benefits of solvers may be negated by increased costs in urban habitats. For example, individuals with better problem-solving performance were found to be less competent in agonistic interactions (Cole and Quinn 2012; Kozlovsky et al. 2014, 2015) or attacked more frequently by their flock-mates (see ***Chapter V***, and Preiszner et al. 2015), although the relationship between problem-solving and competitiveness is not unequivocal (reviewed by Griffin and Guez 2014; Preiszner et al. 2015; Quinn et al. 2016). Thus, stronger competition for food during breeding in urban habitats (Foltz et al. 2015) might reduce the reproductive pay-offs of problem-solving skills. Also, solvers can be more prone to desert their broods in response to disturbance (Cole et al. 2012), which might reduce their success in habitats with frequent disturbance by humans and nest predators. Our present results, however, did not reveal any relationship between sensitivity either to predation risk or to human disturbance and problem-solving performance; moreover, nest desertion after trapping occurred at only one urban nest in our study.

Despite significant individual consistency (at least in the obstacle-removal test where the data enabled meaningful analysis), individual performance did not correlate between the two tasks. This result is in accordance with the view that innovativeness is an emergent property that is shaped by a set of individual traits (Griffin, 2016), thus problem-solving performance can vary across task types and contexts (reviewed by Thornton and Lukas 2012) depending on the specific skills, experiences or other traits required in the task/context. It also aligns with cautionary views that single problem-solving tests cannot be assumed to measure an overall (or any) cognitive capacity without studying the underlying mechanisms (Rowe and Healy 2014; Thornton et al. 2014; Griffin 2016; Reader et al. 2016). In our study, the inconsistency between tasks could have arisen from motivational differences, i.e. solving the obstacle-removal task was imperative to provisioning the chicks, whereas solving the food-acquisition task merely offered extra food items. Alternatively or additionally, the two tests may have assayed at least partially different traits. In the obstacle-removal task, removing the feather usually required few attempts, suggesting that no great physical force or dexterity was needed, but fast solving might have relied on the perception of object permanence, i.e. recognizing that the entrance is still in its original place despite being invisible (Etienne 1984; Emery 2006). In contrast, solving the food-acquisition task required a combination of motor actions and probably the inhibition of ineffective actions such as pecking at the centre of the lid, as in other foraging tasks where performance relies on motor diversity (Griffin et al. 2014; Diquelou et al. 2015), perseverance and/or paying attention to movement cues (Overington et al. 2011a; Thornton and Samson 2012; Audet et al. 2016). A further factor that may have influenced solving performance in our tests is motivation due to variation in the demand for parental care, e.g. in the levels of chicks' hunger. This could explain why solving speed was faster when the parents' total provisioning rate before the test was lower. Motivation may also explain the higher solving success of urban birds in the food-acquisition task, because of the lower availability of natural chick food in urban habitats. We found in the same study setting, that caterpillar biomass, the primary food source for great tit chicks, can be 10-20 times higher in the forest than in the urban habitat (Seress et al. 2018). This may have resulted a higher level of motivation for urban pairs to get additional food, i.e. to solve the food-acquisitioning task. However, our results do not support this assumption, because provisioning rate was not correlated with problem-solving latency in the food-acquisitioning task. Moreover, motivation probably does not explain the poorer performance of forest birds in the obstacle-removal task. Parents of larger broods may be more motivated to remove the obstacle from the nest entrance because larger broods are more valuable and need more feeding. Forest pairs had significantly larger broods than urban pairs, yet the latter were much more successful in problem solving.

Furthermore, because motivation may be greater if the parents have more chicks to feed; the relationship we found between solving speed and the number of fledglings might mean that the latter was influencing the former and not vice versa. The causality of this relationship can only be ascertained by brood-size manipulation experiments; nevertheless, we can speculate that motivational differences are not likely to be the main driver of the correlation between reproductive success and problem-solving performance, for the following reasons. Apart from the correlation between the pair's solving speed and their total provisioning rate, we found no evidence for motivational effects: the pre-test provisioning rate of the solver individuals did not correlate with their problem-solving speed, nor did any other variable such as time of day or chick age which probably reflect the chicks' need. However, motivation is very difficult to quantify or control for in correlational studies (Griffin and Guez 2016). Since our study was not designed to test the role of motivation or other proximate mechanisms underlying performance in the tasks, future experiments could clarify whether urban birds were better solvers due to higher motivation or better spatial cognition or more diverse motor skills.

In sum, we found that better problem-solving performance is associated with higher success in some aspects of breeding, but this relationship did not differ between urban and forest habitats, despite faster solving in the former. If there is no greater net benefit of innovativeness in terms of breeding success in cities than in forests, why are urban birds better solvers? We propose two non-exclusive explanations for this. Firstly, the enhanced benefits of innovativeness for urban birds might manifest in increased juvenile/adult survival. Although Cole et al. (2012) found no difference between solver and non-solver great tits' survival rates in a forest habitat, no systematic study has yet tested whether innovativeness is related to survival in urbanized habitats and whether this effect varies along the urban-rural gradient (Morand-Ferron and Quinn 2015). Secondly, urban birds might be less constrained by the trade-offs that have been implicated between innovativeness and other fitness-related traits, i.e. it is possible that some of the costs of problem solving are actually lower in urban environments. For example, risk sensitivity might be reduced by habituation to humans (Geffroy et al. 2015), whereas being less competitive might be less costly in cities due to altered distribution and abundance of food sources such as bird feeders (Shochat et al. 2006; Tryjanowski et al. 2015), although the latter hypothesis received little empirical support so far (Bókony et al. 2010). A further proposed cost of cognitive skills is the development and maintenance of energetically expensive brain tissue (Kotrschal et al. 2013, 2015); urban birds might afford not paying some of these costs if instead they have more opportunities to explore and learn about their environment and practice various tasks. It has been suggested that experience with diverse foraging substrates in urban habitats enhances motor diversity and thereby problem-solving performance (Diquelou et al. 2015). Exploring how these constraints and trade-offs contribute to innovativeness and the underlying cognitive and other mechanisms in various habitats will further our understanding about how animals succeed in exploiting their environments in our urbanizing world.

CHAPTER IV.

INNOVATIVENESS AND MATE FIDELITY

Abstract

Individual variation in the propensity to express innovative behaviours is increasingly recognized as ecologically and evolutionary significant. A growing number of studies show that more innovative individuals can realize higher breeding success, indicating that innovativeness may be important in mating decisions. Here we investigated whether male and female performance in innovative problem-solving tasks is linked to sexual selection via extra-pair mating behaviour. We observed the problem-solving success of great tit pairs in two tasks at the nest, and related it to the occurrence of extra-pair paternity (EPP) in their broods. In a food-acquisition task, we found no difference in EPP among pairs in which the male solved, pairs in which the female solved, and unsuccessful pairs. In an obstacle-removal task that was solved almost exclusively by females, EPP was more frequent in broods of solver females than in broods of unsuccessful females. These results do not support the hypothesis that the social male's innovativeness influences the female's extra-pair mating behaviour. Instead, they suggest that the female's infidelity covaries positively with her innovativeness. Furthermore, EPP was related to both parents' neophobia such that pairs of highly neophobic individuals were less likely to have EPP than pairs that contained at least one individual with low neophobia. These findings indicate that promiscuity is associated with certain behavioural phenotypes, suggesting that both innovativeness and novelty seeking may facilitate the investment into and/or the exposure to extra-pair mating attempts.

This chapter is a modified version of the research article "Bókony, V., Pipoly, I., Szabó, K., Preiszner, B., Vincze, E., Papp, S., Seress, G., Hammer, T. & Liker, A. (2017) Innovative females are more promiscuous in great tits (*Parus major*). *Behavioral Ecology* 28:579–588."

4.1. Introduction

Based on its plausible links to fitness (see ***Chapter III***, and Preiszner et al. 2017) and mate choice (Boogert et al. 2011), innovativeness can be expected to influence extra-pair mating behaviour. Extra-pair copulations (EPC) occur in many pair-bonding species, and both sexes can play an active role in seeking out and accepting or resisting extra-pair mating partners (reviewed by Westneat and Stewart 2003), although overall it is unclear whether and how the females benefit from EPCs (reviews by Griffith et al. 2002; Wan et al. 2013). A so-far unexplored possibility is that females may be more likely to seek or accept EPCs if they and/or their social mate are poor innovators, for at least two non-exclusive reasons. First, females socially mated to less innovative males may preferentially choose innovative males as extra-pair partners if innovativeness has a heritable component, to increase the chances that the offspring inherit alleles conferring innovative skills. Second, if one or both social parents' lack of innovativeness makes them less successful at breeding, females may compensate for this via cuckoldry either by choosing extra-pair males with any heritable trait that will enhance the offspring's fitness (according to the "good genes hypothesis") or by indiscriminately pursuing copulations with multiple males to ensure diversity in their offspring's genotypes (according to the "genetic diversity hypothesis"). Note that this latter scenario does not depend on the heritability of innovativeness, as females may compensate for low breeding success by any viability gene. For example, in great tits, less innovative females have smaller broods (Cole et al. 2012; Cauchard et al. 2013; Preiszner et al. 2017) possibly because they are less efficient foragers which may limit their egg production and/or reduce their nest attentiveness and consequently their hatching success (Cole et al. 2012; Preiszner et al. 2017). Such females may be more motivated to boost the survival chances of their few offspring by obtaining viability genes through cuckoldry. Both scenarios predict higher incidence of extra-pair paternity (EPP) in broods where the social male is a poor innovator. Furthermore, both scenarios predict that EPP should be highest when both social parents are poor innovators, either because such pairs have the lowest likelihood of passing on "innovativeness alleles" to their offspring, or because they are the least successful in producing and raising viable offspring and thereby are in the most pressing need for viability genes. Thus, this hypothesis predicts that innovativeness is negatively associated with infidelity.

Alternatively, innovativeness may not be the reason for infidelity, but it may alleviate the trade-off between pursuing EPCs and other activities such as foraging. For example, innovative great tits have been suggested to be more efficient foragers as they could deliver the same amount of chick-feeding in shorter time compared to poor innovators (Cole et al. 2012). Such superior time management may allow more opportunity for the innovators to search for extra-pair mating partners (Westneat and Stewart 2003). Consequently, innovative females may be more likely to cuckold their males, whereas innovative males may spend more time seeking EPCs and thereby lose paternity in their own nest because the pursuit of EPCs often comes at the expense of mate guarding (Westneat and Stewart 2003; Patrick et al. 2012; García-Navas et al. 2015). Thus, this second hypothesis predicts the lowest infidelity in pairs that consist of two non-innovative individuals. Alternatively, innovative males may spend more time guarding their females, in which case this second hypothesis predicts the highest infidelity in pairs that consist of an innovative female and a non-innovative male.

A third hypothesis is that innovativeness and infidelity may be indirectly associated via a mediating trait that affects both. A likely such trait is the personality axis related to the responses to novel stimuli (e.g. exploration, neophobia), which has been found to predict both problem-solving success (Sol et al. 2011; Overington et al. 2011a; Griffin and Guez 2014; Quinn et al. 2016) and promiscuity (van Oers et al. 2008; While et al. 2009; Patrick et al. 2012) in several species. For example, more exploratory behaviour may predispose the individuals to more frequently encounter novel problems (Tebbich et al. 2016) as well as opportunities for extra-pair matings (Patrick et al. 2012). Thus, this third hypothesis predicts a positive relationship between innovativeness and EPP due to their association with novelty seeking.

In this study, we confront these 3 hypotheses in great tits. In this species, EPP occurs frequently (typically in 25-50% of nests) and both sexes participate in the pursuit of EPCs (reviewed by García-Navas et al. 2015). Great tit EPP has been found to depend on male and female personality in complicated ways. In a Netherlands population, the highest EPP was observed in assortative (“fast-fast” and “slow-slow”) pairs in terms of exploratory behaviour, which has been interpreted as a strategy for increasing the genetic diversity of offspring (van Oers et al. 2008). In a UK population, the exploratory behaviour of both parents facilitated the male’s paternity outside his social nest (Patrick et al. 2012). Great tits also vary in their propensity to solve novel problem-solving tasks; this variation has been related to exploratory behaviour (Quinn et al. 2016) and breeding success (Cole et al. 2012; Cauchard et al. 2013; Preiszner et al. 2017), although both relationships were contingent upon other factors such as year, sex, and type of task. Here we investigate the relationship between innovativeness and extra-pair mating behaviour by measuring the problem-solving performance of breeding great tits in two tasks in the wild and relating these traits to the occurrence of extra-pair offspring

(EPO) in their broods. We also measured the birds' response to novelty to examine if neophobia mediates any relationship between innovativeness and EPP.

4.2. Methods

We studied great tits breeding in artificial nest boxes in 2012 and 2013 at 4 sites in Hungary; the study sites are described in ***Chapter III*** and Preiszner et al. (2017). Each plot of nest boxes covers ca. 10 ha and they are located on average 14 (range: 3–23) km from each other, separated by agricultural fields unsuitable for great tit nesting. As great tits obtain EPCs typically within a few hundred meters but up to ca. 5 km from their nests (García-Navas et al. 2015), our 4 sites can be treated as 4 populations, i.e. birds within a site could possibly mate with birds from any nest box at that site but are unlikely to mate with birds from another site. At each site, only a fraction of the local great tit population breeds in our nest boxes, so we do not have accurate estimates of population characteristics like breeding density or breeding synchrony; nevertheless we believe that our data constitute a representative sample of the 4 populations.

4.2.1. Collecting DNA samples

In each breeding season, we checked the nest boxes at least every 3-4 days to record the number of eggs and/or chicks. At each nest, when the chicks were on average 6 (range: 5–9) days old (considering the day of the first chick's hatching as day 1), we captured one of the parents in the nest box (excepting a few pairs where one or both parents had already been captured before). Upon capture, we took a drop of blood by puncturing the brachial vein with a 29G needle, and stored the sample in Queen's lysis buffer. We ringed the bird with a unique combination of a metal ring and 3 plastic colour rings, recorded its sex and age (2nd calendar year or older) based on plumage characteristics, and measured its body mass (± 0.1 g) by a spring balance and tarsus length (± 0.1 mm) by a calliper. When the chicks reached the age of 15 (± 2) days, we captured, ringed, blood-sampled, and measured the other parent (if it had not been captured earlier) and the chicks as above. To ensure that chick mortality between hatching and sampling would not bias our results, we collected the dead chicks we found during the nest checks; we took a tissue sample by cutting off a toe and stored it in 96 % ethanol. Thereby we had DNA samples for all hatched chicks in 41 broods, and for 39 out of 50 chicks in total from 6 broods. In these latter broods, we are missing the DNA sample of 1-3 chicks per brood (in total, 11 chicks that died after hatching and their corpse was not found). In 5 out of these 6 broods, we found at least 1 EPO in each, thus our categorization of EPP (i.e. presence of EPO, see below) is correct. In the remaining brood where the DNA sample is missing for a single chick, we found no EPO. This brood was categorized as "EPP absent" in the analyses; however, exclusion of this brood did not change our results qualitatively (as the female solved both tasks).

4.2.2. Behavioural tests

We conducted three behavioural tests (each on a different day) in the same order at each nest when the chicks were 8, 9 and 10 (± 2) days old, respectively. Each test consisted of a 30-minutes baseline observation and an up-to-30-minutes task phase. In 2012, some tests were video-recorded either by a small camera attached to the nest box or by a hand camera placed on a tripod on the ground, whereas some tests were observed by an experimenter from a distance or from a hide using a spotting scope. In 2013, all observations were made using a small camera hidden in a plastic box that was permanently attached to the nest box ca. 15 cm from the entrance (Figure III.1, panel A); these plastic boxes had been installed before the breeding season so the birds were familiar with them by the time of the tests. The type of observation had no significant effect on the outcome of the problem-solving tests, i.e. whether the birds solved or not (Fisher's exact test: $p = 0.435$; number of solved vs. failed tests: spotting scope: 4 vs. 4, camera on tripod: 4 vs. 1, camera on nest box: 4 vs. 6, hidden camera on nest box: 46 vs. 28).

In the first test we assayed the parents' neophobia (i.e. fear of a novel object), as detailed in ***Chapter III***, section 3.2.1. This test allowed the measurement of neophobia in each sex because both parents had the same amount of time available for overcoming their fear of the novel object; latency to first enter the nest box was not correlated within the pairs (Figure IV.1).

Then we conducted two tests designed to assay problem-solving performance. The first was an obstacle-removal task, second problem-solving test was a food-acquisition task as detailed in ***Chapter III***, section 3.2.1.

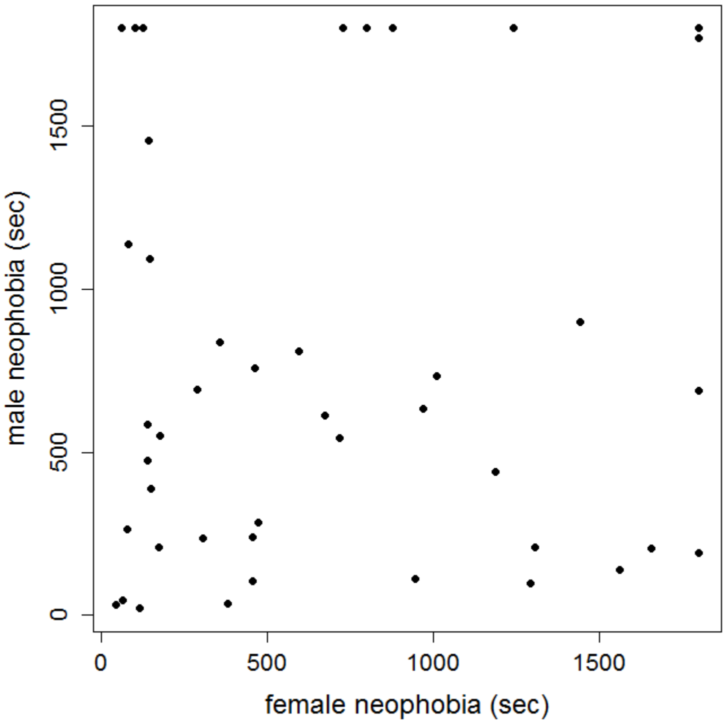

Figure IV.1: Male and female neophobia (latency to enter nest box in the novel object test) were not correlated within the social pair (Spearman rank-correlation, $r_s = 0.05$, $p = 0.737$, $n = 43$ pairs).

4.2.3. Genotyping

Blood and tissue samples were kept at 4°C until analysis. We extracted DNA using silica membrane isolation kits (GeneJET Genomic DNA Purification Kit, ThermoFisher Scientific) and conducted multi-locus genotyping by amplifying 5 microsatellite loci with tri- and tetra-nucleotide repeats (Table IV.1) using multiplex PCR reactions. In a subset of samples with ambiguous results based on the 5 loci, we used 3 additional loci (Table IV.1). Forward primers were labelled with fluorescent dyes (Fam-6, NED, PET, or HEX) on the 5' end; reverse primers contained a GTTT pigtail sequence on their 5' end. PCR reactions were performed in 20 µl volumes, containing 10-30 ng of total genomic DNA template, 1 U of DreamTaq polymerase (Fermentas), 1 × DreamTaq PCR buffer (Fermentas), 1.5 mM MgCl2, 10 pmol dNTPs (Fermentas) and 10 pmol of the respective primer(s). PCR profiles were the following for all loci: initial denaturation at 95°C for 2 minutes, followed by 39 cycles of 95 ºC for 30 sec, 57 ºC for 45 sec and 72 ºC for 45 sec, concluded by a final extension step at 72°C for 7 min. Fluorescent PCR products were scanned by capillary electrophoresis on an Abi 3130 Genetic Analyser (Applied Biosystems); alleles were identified and scored with the Peak Scanner software (Applied Biosystems) by two independent, experienced researchers.

Table IV.1: Observed allele diversity, probability of identity (PI), probability of exclusion with both parents known (PE2) and with only one parent known (PE1), and GenBank accession number of the microsatellite loci used in the study.

Locus	No. of alleles	PI	PE2	PE1	GenBank
PmaGAn27	22	0.011	0.846	0.732	AY260532
PmaTAGAn89	14	0.035	0.719	0.558	HQ263126
PmaTGAn33	16	0.023	0.773	0.630	AY260539
PmaTGAn54	32	0.031	0.733	0.576	HQ263130
PmaTGAn59	20	0.016	0.814	0.686	HQ263131
5 loci combined	**104**	**4.26×10^{-9}**	**>0.999**	**0.994**	
PmaCAn1*	11	0.036	0.715	0.554	AY260530
PmaTAGAn73*	9	0.054	0.653	0.480	HQ263122
PmaTAGAn78*	17	0.014	0.823	0.700	HQ263123
8 loci combined*	**141**	**1.43×10^{-12}**	**>0.999**	**0.999**	

The data are based on 166 adults for the first 5 loci and 20 adults for the 3 loci marked with an asterisk.

Our set of 5 microsatellite markers proved to be highly powerful in detecting parent-offspring relations, as shown by the genetic diversity indices (Table IV.1) calculated with GenAlEx 6.4 (Peakall and Smouse 2012). Note that the birds analysed in the present study were genotyped as part of a larger project which included families that did not participate in problem-solving tests; we calculated the genetic diversity indices for all families (Table IV.1). Both expected and observed heterozygosities for the 5 loci averaged 0.88 (SD = 0.03). The probability of identity when siblings were present was 2.99 × 10-3 for the 5 loci combined and 1.42 × 10-4 for the 8 loci combined. Using MICRO-CHECKER 2.2.2 (Van Oosterhout et al. 2004) we did not find evidence for large-allele dropout and genotyping errors due to stutter bands at any of the 8 loci; null alleles may have been present at one locus (PmaGAn27). Using GENPOP 4.0 (Rousset 2008) we detected no departure from Hardy-Weinberg equilibrium, but significant linkage disequilibrium for 3 pairs of loci (PmaTGAn59 with PmaTAGAn89, PmaTGAn33 with PmaGAn27 and PmaTGAn54; $p < 0.001$). To further validate our 5-loci marker set, we conducted parentage analysis with CERVUS 3.0 (Kalinowski et al. 2007) using the data of 82 candidate fathers and 58 offspring that had no mismatch with their social father's genotype, and providing the mothers' genotype. For each offspring tested, its social father received positive LOD score (i.e. the sum of the log-likelihood ratios at each locus), meaning that this male was more likely to be the genetic father than the other candidate fathers. When more than one candidate fathers had positive LOD scores (n = 26 offspring), the social father always ranked first, i.e. had the highest LOD score. Thus, our 5-loci marker set proved reliable and efficient for identifying EPO and within-pair offspring (WPO).

We identified an offspring as EPO if it mismatched the alleles of the social father on at least two loci but it had no mismatch with the maternal alleles. The number of paternally mismatched loci per offspring ranged between 2 and 7 (most often 4; in 50% of EPO). We could not identify the genetic father of most (23 out of 28) EPO because we did not have DNA samples from all males in each population.

Since EPP may be influenced by within-pair relatedness (Arct et al. 2015), we estimated the coefficient of relatedness (R) for each pair based on our 5-loci marker set using the maximum likelihood method with ML-Relate (Kalinowski et al. 2006). This method accommodates null alleles and is considered to be more accurate than other estimators of relatedness (Milligan 2003). Among the 47 pairs analysed for problem solving, R was estimated to be very low in 35 pairs (zero in 31 pairs; 0.04 – 0.06 in 4 pairs) whereas it was higher in 12 pairs (range: 0.12 – 0.5; mean ± SE: 0.23 ± 0.04). Because a variable with such a skewed distribution was unsuitable for our multivariate models (see below), for the analyses we dichotomized the parents' relatedness as "unrelated" ($R \leq 0.06$) or "related" ($R \geq 0.12$; note that the results did not change when we defined the two respective groups as $R = 0$ and $R > 0$).

4.2.4. Statistical analyses

We analysed the relationship between EPP in the social nest and problem-solving success separately for the 2 tasks, because the individuals' solving latency did not correlate between the obstacle-removal task and the food-acquisition task (for details see ***Chapter III.***). Although some pairs were tested for problem solving in more than one breeding episode, we analysed only the first test for each pair, i.e. when both parents encountered each test situation for the first time. Sample size varies across the analyses due to a few missing data for each behavioural test.

In all analyses we expressed EPP as the presence/absence of EPO, and we categorized problem-solving success according to the sex of the solver parent as male solved, female solved, or neither parent solved (birds that did not solve because they did not show up on the nest box during the test were considered non-participating and were not analysed; see Preiszner et al. 2017). We used these categorical variables instead of numerical metrics because the distribution of the number of EPO was strongly skewed (Figure S.IV.1) and the latency to solve each task had bimodal distribution due to the fact that non-solvers had to be assigned the maximal latency of 30 minutes (Preiszner et al. 2017). Nevertheless, to ensure that our main results were not sensitive to the dichotomization of the variables, we report an additional set of analyses in which we tested the relationship between the number or proportion of EPO and the latency to solve each task by Spearman rank-correlations (Table S.IV.1). Also, note that in both problem-solving tests, female solving success is unknown in pairs in which the male solved, and similarly, male solving success is unknown in pairs in which the female solved; thus our assessment of performance is not independent between the male and female of a pair. Throughout the analyses, we treated the birds whose mate had solved as missing data; however, to show that our main results were not sensitive to the exclusion of these birds, we report an additional set of analyses in which we tested the relationship between EPP and solving latency by including the birds whose mate solved as censored observations (Table S.IV.2). These two sets of supplementary analyses (Tables S.VI.1-S.VI.2) demonstrate that our results are robust.

For each task, first we tested the relationship between EPP (presence/absence of EPO) and sex of solver parent using Fisher’s exact test. Secondly, we analysed each task in a generalized linear mixed-effects model with quasi-binomial error distribution and logit link function, using EPP (presence/absence of EPO) as the dependent variable, the sex of solver parent as a fixed factor, and site as a random factor to control for any site-specific variation in EPP (e.g. due to differences in breeding density and breeding asynchrony; Wan et al. 2013). Thirdly, we used this mixed-model framework to perform a forward-stepwise model-selection procedure to ensure that potential predictors of EPP did not confound our results. We used the forward approach because it performs better than the backwards method when the number of potential predictors is relatively high (Derksen et al. 1992). During this procedure, every potential predictor is evaluated separately in the first step, and the one with the lowest P-value is retained for the second step, in which all the other predictors are evaluated each in a separate model that also includes the predictor selected in the first step, and so on. Model selection ends when no further predictor can be added either because the added predictor(s) would be non-significant ($p > 0.05$) or because the model would be over-parameterized (i.e. no degrees of freedom left for estimating within-group variance). Using this approach, we tested the effects of the sex of solver parent, male age, and within-pair relatedness as fixed factors; male tarsus length, lay date of the first egg (number of days since 1st April), and the neophobia of both parents as covariates, and the interaction between male and female neophobia.

Additionally, we conducted 2 further analyses to investigate the potential consequences of EPP for paternal care and offspring fitness in our study system. To test whether female infidelity was related to the level of parental care provided by the social male, we compared male chick-feeding rate between nests with and without EPO. We calculated male chick-feeding rate as the number of times the male entered the nest box during each 30-minutes baseline observation in the 3 behavioural tests, divided by the number of chicks. We used chick-feeding rate (i.e. 3 repeated measures per male) as dependent variable in a single linear mixed-effects model with brood ID nested within site as random factors, and EPP, the order of observation (first/second/third), and timing of capture (whether or not the male was captured on the nest before the observations) as fixed factors, and the date of observation and time of day as covariates. Because the latter two effects were non-significant, we omitted them from the model presented here. Finally, to test whether female infidelity was beneficial in terms of offspring fitness, we compared the survival and size of EPO and WPO within the nests that contained at least one EPO. The proportion of chicks surviving to the age of ringing (shortly before fledging) was compared between EPO and WPO with Fisher's exact test of independence (mixed-effects modelling was not feasible here because chick mortality was very low, thus in most nests there was zero variance in survival). The chicks' tarsus length and body mass measured upon ringing was each used as dependent variable in a linear mixed-effects model with brood ID nested within site as random factors, EPP as a fixed factor, and date of measurement (number of days since 1st May) as a covariate. For body mass, time of day (minutes since 7:00 a.m.) was also added as a covariate. Both models also included the chicks' age at measurement as a covariate and the ID of the experimenter who took the measurement as a fixed factor; however, these 2 effects were non-significant and therefore omitted from the models presented here. All analyses were run with R 3.2.2, using the 'nlme' package for mixed-effects models (Pinheiro et al. 2016).

4.3. Results

Out of 47 broods, EPO were present in 15 (31.91 %). The number of EPO was 1 in 8 broods and 2 in 4 broods; the remaining 3 broods contained 3, 4, and 5 EPO. Out of a total of 445 offspring, 28 were EPO (6.29 %), representing 8.33–60 (mean: 22.96 ± 4.36 SE) % of offspring within each brood that contained EPO.

In the obstacle-removal task, 22 females and 3 males solved whereas 18 pairs were unsuccessful. In these 3 groups, the percent of broods containing EPO was 45.5 % (10/22), zero (0/3), and 11.1 % (2/18), respectively; this association between EPP and the sex of solver parent was significant (Fisher's exact test: $p = 0.040$). The mixed-effects model confirmed that EPP was more likely in broods of solver females than in broods of unsuccessful pairs (Table IV.2, Figure IV.2); the estimated effect of solver males was not significant but had very high uncertainty because EPP was zero in the broods of all 3 solver males (Table IV.2; see supplementary Table S.IV.3 for a more robust test of this effect).

Table IV.2: Odds ratios (*OR*) of having extra-pair offspring in the brood, in relation to the sex of solver parent in 2 problem-solving tasks.

Task	Model parameters	*OR* (95% CI)	df	*t*	*p*
Obstacle-removal[a]	Unsuccessful pairs	0.12 (0.03, 0.60)	37	-2.77	0.009
(*n* = 43 pairs)	Pairs with solver female[a]	6.67 (1.14, 38.9)	37	2.20	0.034
	Pairs with solver male[a]	<0.01 (0, ∞)	37	<0.01	>0.999
Food-acquisition[b]	Unsuccessful pairs	0.76 (0.21, 2.77)	35	-0.42	0.681
(*n* = 41 pairs)	Pairs with solver female[a]	0.35 (0.05, 2.28)	35	-1.10	0.278
	Pairs with solver male[a]	0.50 (0.08, 3.21)	35	-0.73	0.468

Odds ratios and their 95% confidence intervals (CI) were calculated from the parameter estimates of linear mixed-effects models with quasi-binomial error distribution and site as random factor.

[a] These estimates express the differences from the unsuccessful pairs.

Table IV.3: Final model of extra-pair paternity in relation to the sex of solver parent in the obstacle-removal task; *n* = 41 pairs.

Model parameters	*OR* (95% CI)	df	*t*	*p*
Intercept (unsuccessful pairs, 2012)[a]	3.58 (0.02, 644.7)	30	0.48	0.634
Pairs with solver female[b]	71.82 (2.77, 1858.9)	30	2.58	0.015
Pairs with solver male[b]	<0.01 (0, ∞)	30	<0.01	>0.999
Second study year (2013)[b]	<0.01 (0, 0.12)	30	-2.98	0.006
Male tarsus length[c]	0.19 (0.04, 0.80)	30	-2.25	0.032
Male neophobia[c]	1.28 (1.06, 1.56)	30	2.61	0.014
Female neophobia[c]	1.18 (0.99, 1.41)	30	1.86	0.073
Male × female neophobia[d]	0.98 (0.96, 1.00)	30	-2.41	0.022

Odds ratios (*OR*) and their 95% confidence intervals (CI) were calculated from the parameter estimates of a linear mixed-effects model with quasi-binomial error distribution and site as random factor.

[a] The intercept is the odds ratio of having extra-pair offspring in the broods of unsuccessful pairs in the first study year, for the shortest male tarsus length (18.3 mm) and zero neophobia in both sexes.

[b] These estimates express the differences from the intercept.

[c] These estimates express the change in the odds ratio of having extra-pair offspring in the brood in response to 1-mm increase in tarsus length or 1-min increase in neophobia.

[d] Interaction between male and female neophobia; see Figure IV.3 for interpretation.

The forward model selection identified 3 further significant predictors of EPP (Table IV.3): EPP was more frequent in the first study year than in the second, less frequent in broods of males with longer tarsi, and depended on the parents' neophobia. The latter effect was an interaction between male and female neophobia, such that EPP was least frequent when both parents were highly neophobic (Figure IV.3). The presence of EPP was not related significantly to male age, first egg date, and within-pair relatedness (Table S.IV.4). Finally, the relationship between EPP and female solving success remained significant when both variables were used as numeric variables in a non-parametric correlation (Table S.IV.1).

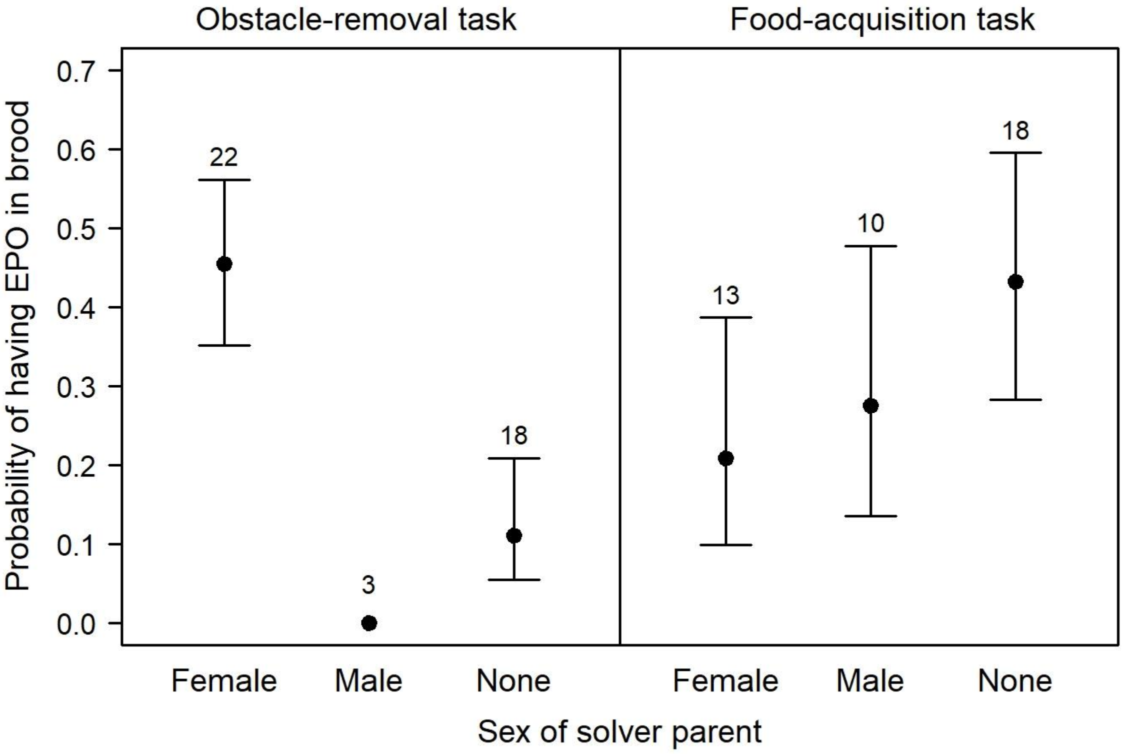

Figure IV.2: Probability of having extra-pair offspring (EPO) in the brood, in relation to the sex of solver parent in two problem-solving tasks, as estimated by the models in Table IV.2. Whiskers correspond to ± 1 SE; numbers above the error bars denote sample sizes. Note that there was no variance in EPP among solver males in the obstacle-removal task.

The distribution of the sex of solver parent differed between the 2 problem-solving tests (all pairs, Fisher's exact test: $p = 0.049$) such that the solver parent was more often the male in the food-acquisition task (43.5% of successful pairs) than in the obstacle-removal task (12% of successful pairs; Fisher's exact test: $p = 0.022$). In the food-acquisition task, 13 females and 10 males solved whereas 18 pairs were unsuccessful. In these 3 groups, the percent of broods containing EPO was 30.8 % (4/13), 30.0 % (3/10), and 38.9 % (7/18), respectively; thus EPP was not associated with the sex of solver parent in this task (Fisher's exact test: $p = 0.840$). The mixed-effects model corroborated this result (Table IV.2, Figure IV.3); inclusion of any other potential predictor of EPP in the model did not change qualitatively the effect of the sex of solver parent ($p > 0.345$). Furthermore, the relationship between EPP and solving success of both sexes remained non-significant when used as numeric variables in non-parametric correlations (Table S.IV.1).

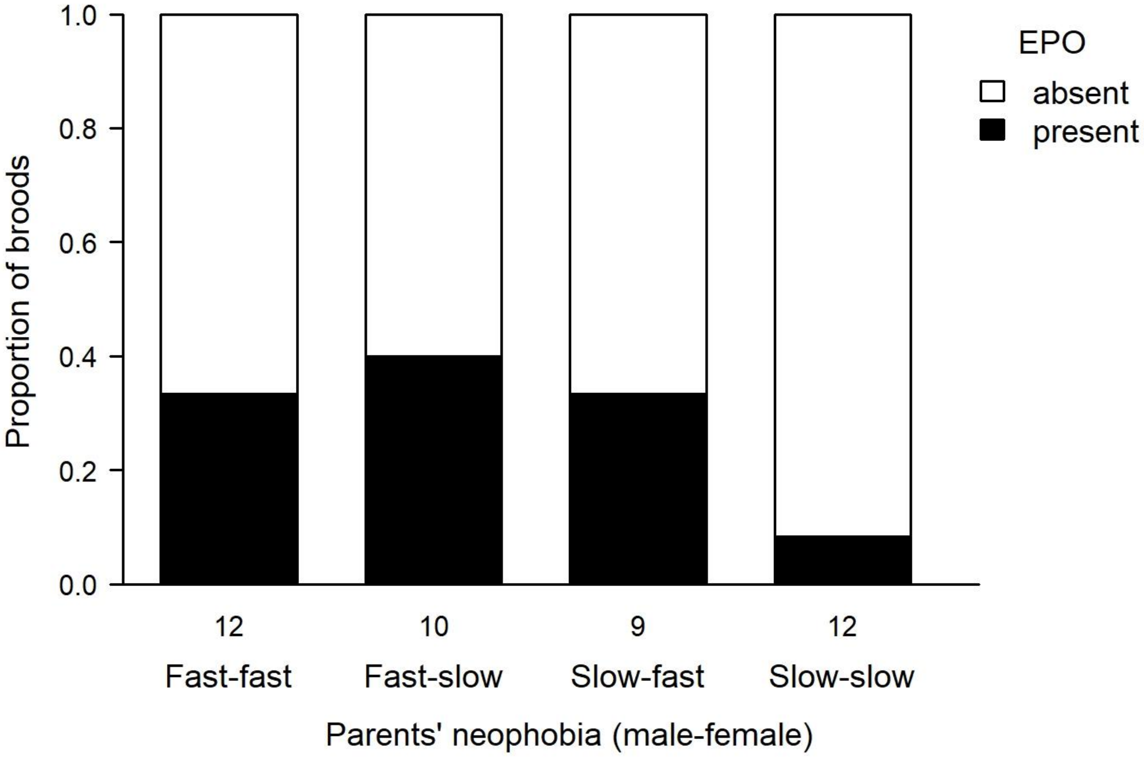

Figure IV.3: Proportion of broods containing extra-pair offspring (EPO), in relation to the rearing parents' neophobia. For illustrative purposes, neophobia of each sex was dichotomized as "fast" (i.e. shorter than median latency to enter nest box in presence of novel object) or "slow" (≥ median latency). Numbers below the bars denote sample sizes.

Male chick-feeding rate increased across the 3 observations and was reduced if the male had been captured before the tests, but did not differ significantly between broods with and without EPP (Table IV.4); the interaction between EPP and the order of observation was not significant ($p = 0.359$). In the 15 broods with EPP, 2 out of 93 WPO (2.15 %) and 1 out of 28 EPO (3.57 %) died before fledging (Fisher's exact test: $p = 0.549$). Neither tarsus length nor body mass differed significantly between EPO and WPO (Table IV.5).

Table IV.4: Male chick-feeding rate in relation to extra-pair paternity; *n* = 47 males.

Model parameters	*b* ± SE	df	*t*	*p*
Intercept[a]	0.44 ± 0.11	91	3.86	<0.001
EPO[b] present in brood	0.12 ± 0.12	42	0.96	0.340
Second observation	0.26 ± 0.07	91	3.54	0.001
Third observation	0.20 ± 0.07	91	2.64	0.010
Male captured before tests	-0.29 ± 0.12	91	-2.49	0.014

Parameter estimates (*b*) with standard error (SE) are shown for a linear mixed-effects model with brood nested in site as random factors.

[a] The intercept is the estimated average of the non-captured males' *per capita* chick-feeding rate in the first 30-minutes baseline observation in nests with no extra-pair paternity; the remaining estimates express the differences from this group.

[b] EPO: extra-pair offspring

Table IV.5: Fledgling size in extra-pair offspring (EPO) and within-pair offspring (WPO); *n* = 118 chicks in 15 broods.

Dependent variable	Model parameters	*b* ± SE	df	*t*	*p*
Tarsus length	Intercept (WPO)[a]	18.78 ± 0.52	102	36.39	0.000
	EPO[b]	0.08 ± 0.13	102	0.62	0.538
	Date[c]	0.04 ± 0.02	10	1.99	0.074
Body mass	Intercept (WPO)[a]	12.36 ± 1.39	101	8.90	0.000
	EPO[b]	-0.07 ± 0.25	101	-0.26	0.796
	Date[c]	0.09 ± 0.04	10	2.11	0.061
	Time of day[c]	0.01 ± 0.002	101	3.00	0.003

Parameter estimates (*b*) with standard error (SE) are shown for linear mixed-effects models with brood nested in site as random factors.

[a] The intercept is the estimated average size of WPO on the first day (1st May) and, for body mass, at the start of the day (7:00 a.m.).

[b] These estimates express the difference in average size between EPO and WPO.

[c] These estimates express the change in average fledgling size in response to a 1-unit change in the predictor variable (1 day for date, 1 min for time of day).

4.4. Discussion

To our knowledge, this is the first study scrutinizing the relationship between innovativeness and extra-pair mating. While we have identified several significant predictors of EPP, partially in agreement with previous findings from other great tit populations (Blakey 1994; Verboven and Mateman 1997; van Oers et al. 2008; Patrick et al. 2012), our study yielded the novel finding that the females' infidelity is related to their problem-solving success in a task which was previously shown to be ecologically relevant and repeatable (see ***Chapter III.***). In males, which were more likely to solve another task, we found no relationship between innovativeness and EPP in the social nest. Below, we discuss these findings in light of the 3 hypotheses that we introduced.

Our first hypothesis was that male innovativeness decreases his mate's tendency towards infidelity; however, we found no evidence for the prediction that females mated to males with poor problem-solving performance cuckold more often than females mated to innovative males. In the food-acquisition task, which was solved more often by males than was the other task, there was no relationship between the sex of solver parent and EPP, i.e. pairs with solver males were equally likely to have EPO as unsuccessful pairs (in which the male was unsuccessful) as well as pairs with solver females (in which the males' solving performance is not known but, given that their females solved, these males might have been slower than solver males). In the obstacle-removal task, the sample size for solver males was very small, preventing their powerful comparison to unsuccessful males. However, we also predicted that EPP should be highest in unsuccessful pairs who may be the most in need of "good genes" (genes for either innovativeness in particular or viability in general) for their offspring, whereas pairs in which at least one of the parents is innovative can pass on "innovativeness alleles" and/or produce viable offspring even without cuckolding. This prediction was not supported by our data either, because in the food-acquisition task, unsuccessful pairs did not differ from successful pairs in EPP, whereas in the obstacle-removal task, males of unsuccessful pairs were cuckolded significantly less, not more, than were males whose mate had solved. Thus, our results do not support the idea that lack of innovativeness would drive females to compensate by obtaining extra-pair fertilizations. A potential explanation for this may be low heritability of problem-solving performance, as has been found in another great tit population (Quinn et al. 2016), and/or limited effect of male innovativeness on breeding success (Cole and Quinn 2012; Preiszner et al. 2017); in both cases, females would benefit little from taking into account their social mate's innovativeness during their extra-pair mating decisions. Alternatively, whether or not innovativeness is a relevant, and even heritable, trait of males, it is possible that female promiscuity is not driven by genetic benefits at all. In our study, although smaller males were more likely to get cuckolded, EPO did not grow larger in the nest than WPO, which does not support that cuckolding females were compensating for their social male's quality. In line with this, several studies on great tits (Krokene et al. 1998; Strohbach et al. 1998; Lubjuhn et al. 1999; García-Navas et al. 2015) and other species (reviewed by Akçay and Roughgarden 2007) failed to find evidence for the hypothesized genetic benefits of EPP. Instead, some studies suggest that female promiscuity has evolved by selection on male promiscuity and genetic correlation between the sexes, while being neutral or even costly to females (i.e. the "intersexual antagonistic pleiotropy" hypothesis; reviewed by Forstmeier et al. 2014).

Our second hypothesis was that innovativeness of females (and perhaps also males) increases their own tendency towards infidelity. We found no such effect in the food-acquisition task; however, in the obstacle-removal task, which was solved almost exclusively by the females, we found that solver females were significantly more likely to have EPO than non-solver females. This result was robust to site and year effects, and remained significant when we took into account the parents' other phenotypic traits that are related to EPP. In our study system, performance in the obstacle-removal task, but not in the food-acquisition task, was positively correlated with the number of chicks raised per brood (see ***Chapter III.***), suggesting that problem-solving performance as measured in the obstacle-removal task was a trait relevant to fitness, at least during the breeding season. The higher reproductive output of solver females in 3 different populations of great tits (Cole and Quinn 2012; Cauchard et al. 2013; Preiszner et al. 2017) has been interpreted as a result from more efficient foraging early in the breeding season when food is still scarce (Cole and Quinn 2012). Our present finding might be attributed to the same effect, i.e. solver females may be more likely to obtain EPP due to better time management during their fertile period, if searching for and evaluating extra-pair males is traded-off against foraging time (Slagsvold and Lifjeld 1997; "the constrained female hypothesis" in Hoi-Leitner et al. 1999; and see also Westneat and Stewart 2003). Whether females pursue EPP for some net benefit or merely due to genetic correlation with related traits in males, this scenario could explain the higher promiscuity of solver females because they would be less constrained in their pursuit. Trade-off with foraging might also explain the year effect we found, as the spring of 2013 was unusually cold with snow cover in early April, which could have made it challenging for great tits to find enough resources for getting prepared for breeding and, at the same time, foray for extra-pair mating opportunities. Alternatively, innovative females might be better equipped to bear another putative cost of EPP, i.e. punishment by their social mate. For example, if males respond to female infidelity by providing less help at the nest, as has been found in some species (reviewed by Whittingham and Dunn 2001), solver females may be more ready to afford this cost if they are more efficient in parental care than non-solvers. We found no evidence that male chick-feeding rate was reduced in broods with EPP, although a strong test of the punishment hypothesis would require a within-male comparison of parental care with and without EPP, so we cannot exclude the possibility that the high fidelity of non-solver females was due to their need to avoid male punishment. Alternatively, it is also possible that cuckolding females had higher problem-solving success not because they were more innovative but because their males reduced their nest attentiveness as punishment, leaving the female to solve the tasks. However, this explanation is less likely because the reward of solving was related to parental care in both tasks, whereas male solving was rare in one of the tasks but not in the other.

Our third hypothesis was that the relationship between innovativeness and infidelity is mediated by a third variable, i.e. by the tendency for novelty seeking. However, the relationship we found between female innovativeness and EPP cannot be explained merely by personality affecting both, because both neophobia and solving success were significant predictors in the same model, and solving latency did not correlate significantly with neophobia (Table S.IV.5, Figure S.IV.2). Nevertheless, we found an effect of the parents' neophobia such that "slow-slow" pairs were the least likely to have EPO. Interestingly, this is the opposite of what has been reported from a great tit population in the Netherlands (van Oers et al. 2008), whereas in a UK population neither parent's exploratory behaviour nor their interaction explained the presence of EPO in their own broods (Patrick et al. 2012). Because our study was not designed to investigate behavioural syndromes, we do not know to what extent the neophobia measured in our novel object test is related to exploratory behaviour in particular and personality in general; nevertheless, responses to a novel object and to a novel environment were found to be correlated in great tits (Groothuis and Carere 2005; Herborn et al. 2010). Assuming that neophobia reflects a personality trait with non-negligible heritability similarly to exploratory behaviour (Groothuis and Carere 2005), a link between low neophobia (or fast exploration) and promiscuous behaviour might be explained by pleiotropy, in accordance with the genetic correlation hypothesis of EPP (Forstmeier et al. 2014). Thereby "fast" individuals of both sexes may invest more into cuckoldry than slow individuals, which would explain the higher EPP in broods where the female and/or the male is "fast", as the former would be genetically predisposed to infidelity while the latter might trade off mate guarding for EPC, leaving more opportunity for their females to pursue, or fall victim to, extra-pair mating attempts. Although we have no data yet to validate this idea, it is noteworthy that both our main results, i.e. the effects of innovativeness and neophobia on EPP, seem more compatible with the genetic correlation hypothesis than with any net benefit of female infidelity.

Further potential explanations might have contributed to our findings. On the one hand, if success in the obstacle-removal task was related to a more general problem-solving capacity, solver females could have been better than non-solvers at solving social or cognitive problems associated with EPCs, such as evaluation of male quality or outsmarting the mate-guarding male (West 2014). The idea of an EPC-driven cognitive arms race between males and females has been supported by the inter-specific relationship between EPP and sex differences in brain size (Garamszegi et al. 2005). However, the role of cognition in problem solving (Griffin and Guez 2016) and the evidence for a general intelligence in animals (Thornton and Lukas 2012) is equivocal, and individual performance did not correlate between our two problem-solving tasks (see ***Chapter III.***). Thus, it remains unclear if success in our obstacle-removal task reflected the females' general ability to solve other problems, including the skills facilitating EPCs. On the other hand, a relationship between infidelity and innovativeness might arise due to variation in individual quality, because the latter may affect not only EPP (i.e. the need to get high-quality genes) but also problem solving. However, the direction of this relationship is difficult to predict, since low-quality individuals may be more motivated and reliant on novel behaviours (Cole and Quinn 2012), but high-quality individuals may have more capacity for innovations (Bókony et al. 2014). Because empirical evidence for these conflicting effects is inconclusive in general (Griffin and Guez 2014) as well as in great tits (Cole and Quinn 2012; Quinn et al. 2016), we can speculate that individual quality is not likely to have driven solving success in our tasks. Finally, because our assessment of problem-solving performance was not independent between the male and female of a pair, it is theoretically possible that the relationship we found between female innovativeness and EPP was driven by variation in male innovativeness. This is unlikely to be the case, however, because our analyses of the continuous-scale variables consistently showed an effect of females and no effect of males in the obstacle-removal task (Tables S.VI.1-S.VI.2).

To summarize, we found that innovativeness predicted the occurrence of EPO in great tits' broods, but not as expected based on the assumption that females cuckold for genetic benefits to compensate for poor parental innovativeness. Instead, our results suggest that innovative females are more promiscuous, possibly because they are less time-constrained, whereas neophobic pairs are more faithful, perhaps due to a pleiotropic link between personality and infidelity. Thus, emergent behavioural phenotypes may have complex effects on mating decisions and thereby on fitness.

CHAPTER V.

INNOVATIVENESS AND SOCIAL SUCCESS

Abstract

In group-living animals, individuals may benefit from the presence of an innovative group-mate because new resources made available by innovators can be exploited, for example by scrounging or social learning. Consequently, it may pay off to take the group-mates' problem-solving abilities into account in social interactions such as aggression or spatial association, e.g. because dominance over an innovative group-mate can increase scrounging success, while spatial proximity may increase the chance of both direct exploitation and social learning. In this study, we tested whether the individuals' innovation success influences their social interactions with group-mates in small captive flocks of house sparrows. First, we measured the birds' actual problem-solving success in individual food-extracting tasks. Then we manipulated their apparent problem-solving success in one task (by allowing or not allowing them to open a feeder repeatedly) while a new, unfamiliar group-member (focal individual) had the opportunity to witness their performance. After this manipulation, we observed the frequency and intensity of aggression and the frequency of spatial associations between the focal individuals and their manipulated flock-mates. Although flock-mates behaved according to their treatments during manipulations, their apparent problem-solving success did not affect significantly the focal individuals' agonistic behaviour or spatial associations. These results do not support that sparrows take flock-mates' problem-solving abilities into account during social interactions. However, focal individuals attacked those flock-mates more frequently that had higher actual problem-solving success (not witnessed directly by the focal individuals), although aggression intensity and spatial association by the focal birds were unrelated to the flock-mates' actual success. If this association between flock-mates' actual innovativeness and focal individuals' aggression is not due to confounding effects, it may imply that house sparrows can use more subtle cues to assess the group-mates' problem-solving ability than direct observation of their performance in simple foraging tasks.

This chapter is a modified version of the research article "Preiszner, B., Papp, S., Vincze, E., Bókony, V. & Liker, A. (2015) Does innovation success influence social interactions? An experimental test in house sparrows. Ethology 121: 661-673."

5.1. Introduction

Innovativeness, a trait associated to cognition might be linked to social performance of individuals. Although a few hypotheses have been formulated about the social costs/benefits of innovativeness (see ***Chapter I***, section 1.4.), correlative studies testing these produced mixed results. Individual performance in problem-solving tasks, a proxy for innovativeness, was not related to dominance rank in several birds and mammals (Wiley 1991; Bouchard et al. 2007; Pongrácz et al. 2008; Benson-Amram and Holekamp 2012), whereas subordinates were either less innovative (Boogert et al. 2006, 2008) or more innovative than dominants in others (Laland and Reader 1999a; Reader and Laland 2001; Cole and Quinn 2012; Thornton and Samson 2012). Moreover, the performance of individuals in cognitive tasks may be altered by the presence of group-mates, implying that correlative results might be confounded by the study conditions (Nicol and Pope 1999; Drea and Wallen 1999; Overington et al. 2009a). Similarly, the relationship between innovativeness and social associations is poorly known. For example, in mixed wintering flocks of three Paridae species, more central individuals of the social network were more likely to use novel food sources, suggesting the importance of associations in information transfer (Aplin et al. 2012). On the other hand, in another songbird species, the starling (*Sturnus vulgaris*) the association network did not predict the spread of innovations (Boogert et al. 2008). To our knowledge, no study has experimentally tested whether aggressive and affiliative relationships are causally influenced by the innovativeness of group-mates.

In this study, we conducted an experiment to investigate whether individuals behave differently towards their innovative and non-innovative flock-mates in the house sparrow. This species is one of those with the highest number of foraging innovations reported among wild birds (see supplementary material of Overington et al. 2009b) and also readily solves foraging tasks in the lab (Liker and Bókony 2009; Bókony et al. 2014). In the non-breeding season, sparrows live in flocks and often establish close to linear dominance hierarchies with frequent aggressive interactions (Anderson 2006). They typically do not engage in affiliative interactions but they maintain spatial associations with preferred flock-mates such as siblings (Tóth et al. 2009b). During social foraging, they often use aggressive scrounging to obtain food from their flock-mates and more dominant birds scrounge more frequently (Liker and Barta 2002), whereas individuals with superior learning ability are more likely to forage as producers (Katsnelson et al. 2011).

Specifically, we tested the following predictions in house sparrows. Firstly, because dominance facilitates scrounging, individuals may attempt to achieve dominance over their innovative flock-mates by behaving more aggressively against them. Thus, individuals perceived as more successful innovators should be attacked more often and/or more intensively by their flock-mates. Secondly, because spatial association enables social learning and the less frequent non-aggressive scrounging, we expect that sparrows tend to associate more with their more innovative flock-mates. To test these predictions, first we measured the individuals' actual problem-solving success in three foraging tasks, and then manipulated their apparent innovation success in the eyes of an unfamiliar conspecific. Finally, we tested whether the aggressive and non-aggressive social behaviours of these unfamiliar flock-mates differ towards the birds with apparently different innovative ability.

5.2. Methods

This study is part of a more general project that explores the causes and consequences of behavioural flexibility in birds (Bókony et al. 2014; Papp et al. 2015; Vincze et al. 2015, 2016). The experiment presented here was built on this previous work and utilized some of the data in them. However, the papers report entirely different sets of analyses investigating separate research questions, and there is no overlap in the presented results. Methods shared by these studies are repeated here to make all relevant details readily available.

During the procedures described here, 19 out of 110 birds (17.3%) died for unknown reasons. For details and discussion on possible causes, see ***Chapter VI***.

5.2.1. Subjects and overall experimental design

In January - March 2012, we captured 10-14 house sparrows each week over 8 weeks using mist-nets (Ecotone, Gdynia, Poland); each week we sampled two capture sites 6.8–69.2 (mean ± SE = 32.7 ± 6.8) kilometres apart. As house sparrows are very sedentary (Anderson 2006; Liker et al. 2009), it is likely that birds from the two capture sites sampled in a given week were not familiar with each other. Upon capture we measured body mass (± 0.1 g using a Pesola spring balance) and tarsus length (± 0.1 mm using dial callipers). Birds were brought into captivity and housed for 3 weeks.

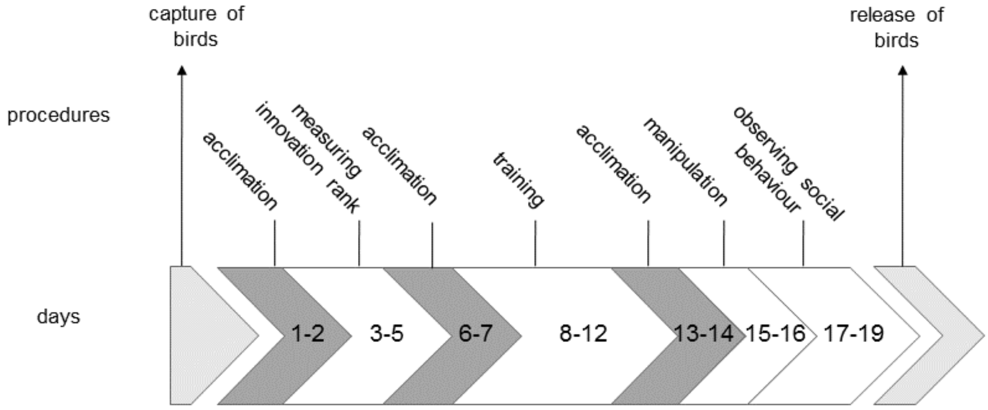

Figure V.1. Timeline of the procedures in the study applied each week group of sparrows. During the training period the subsequent flock-mates learned to use a feeder used throughout the manipulation. In the manipulation period we manipulated the information available for focal individuals about their flock-mates' problem-solving performance.

The outline of the study is illustrated in Figure V.1. In short, first we assessed the birds' problem-solving performance in 3 tasks in which they were tested individually. Then some of the birds were trained to use a novel feeder, while the others were not presented with this task. We used this latter group of birds as focal individuals in the next part of the study, in which we manipulated the information available to the focal individuals about the problem-solving performance of the trained birds (which were unfamiliar to the focal individuals) so that some appeared successful while others appeared unsuccessful. Up to this phase of the experiment the birds were kept in individual cages. Finally, we observed the focal individuals' aggressive and affiliative behaviours towards the manipulated birds while they were allowed to interact in small flocks. We describe each of these steps in detail below.

5.2.2. Measuring the birds' actual problem-solving performance

After 1-2 days of acclimation following capture, we tested the performance of each individual in three food-extracting tasks (Figure V.2, panels A-C) over three days. These procedures were the same as detailed by Bókony et al. (2014), therefore here we provide a short description only. Birds were kept in individual cages, and those captured from different localities were visually separated by opaque plastic sheets to prevent them from getting visual information about each other; and during the tests, every bird was visually blocked from the others. Each test took place in the morning after 90 minutes fasting, and we recorded each bird's latency to solve the task (i.e. time elapsed from the start of test until the bird started to feed) over 90 minutes per task. As individual performance across the three tasks was weakly but significantly repeatable (ICC = 0.153, 95% confidence interval: 0.033 - 0.286, $F_{97,196} = 1.54$, p = 0.006; for further details see Bókony et al. 2014) , from these data we calculated innovation rank for each individual as the mean of the 3 within-task ranks of problem-solving latencies; higher innovation rank means faster problem-solving performance.

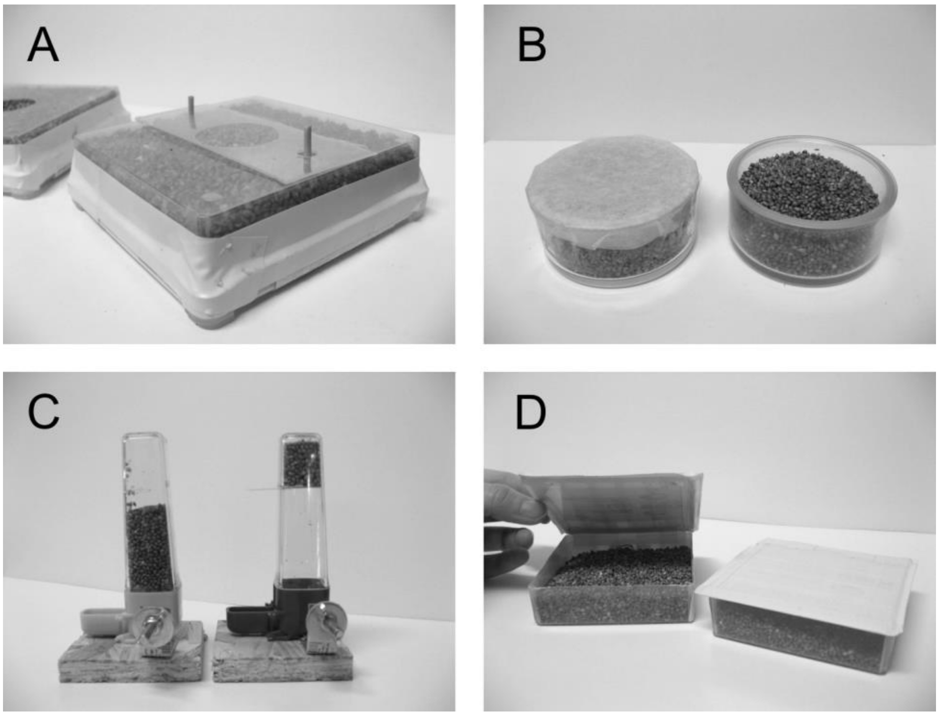

Figure V.2. Feeders used in the experiment. A) Problem-solving feeder 1 closed in the front, open in the back. B) Problem-solving feeder 2 closed on the left, open on the right. C) Problem-solving feeder 3 open on the left, closed on the right. D) Training feeder open on the left, closed on the right. Figure originally published in Behavioral Ecology (Bókony et al. 2014).

5.2.3. Training in a new task

After the third problem-solving test, birds were transferred into another room where they were allowed to acclimate for two days in individual cages. On days 8-12, we presented a subset of birds (n = 72; hereafter referred to as “flock-mates”) with a fourth task repeatedly in a total of 19 training sessions, as detailed by Bókony et al. (2014), to train them to use a special feeder (henceforth “training feeder”). This training feeder was an 8.5 × 8.5 × 2.5 cm white plastic box with one transparent side and a lid on the top (Figure V.2, panel D); birds had to insert their beak and head under the lid and push it up to reach the food. The training feeder did not remain open after the bird first fed from it; instead, it had to be opened every time to peck a seed. There were four 30 minutes training sessions each day (excepting the last day) between 9:00 - 16:00, each preceded by 60 minutes fasting, and the behaviour of the birds was observed during each training session from behind a one-way window. Birds that did not open the training feeder by the 10th training session (n = 18) were allowed to remain in visual contact with one of their neighbours that could already use the feeder; if then the bird fed from the training feeder successfully in two consecutive training sessions (n = 6), we re-inserted the opaque sheet again between the cages. Twelve birds did not learn this task by the end of the training period; in the subsequent stage of the experiment 5 of these birds were allocated to treatment groups where there was no need for the trained skill (see below). Between the training sessions, birds were allowed to feed from the training feeder with the lid fixed in open position by a small transparent cup.

The rest of the birds (n = 26, hereafter referred to as "focal individuals") were not trained; they were kept visually separated from the trained birds, with ad libitum food available in their cages from a transparent plastic dish (7.5 cm diameter, 3.5 cm high; henceforth "feeder dish"). After the 19th training session, all birds were individually colour marked on the top of their head using non-toxic marker pens (Decopainter, Marabu Co., Bietigheim-Bissengen, Germany) in order to facilitate individual recognition by the observer in the subsequent stage of the experiment, and they were placed into new cages as follows.

5.2.4. Manipulation of Apparent Problem-Solving Performance of the Trained Birds

On day 12, ten birds were selected for further procedures randomly with some constraints detailed below. These birds participated in 7 sessions over 2 days in which we manipulated the information about the trained birds' (i.e. flock-mates') innovation success to the untrained birds (i.e. focal individuals). The 10 birds were divided into 2 "flocks", each consisting of 5 members of the same sex; note that the flock-mates still remained in separate cages during the manipulation. In each flock the 4 trained flock-mates had been captured from the same location, whereas the fifth (the focal individual) had been captured from a different site. Due to the visual separation during the earlier innovation tests and training, focal individuals had no previous experience of their assigned flock-mates' actual problem-solving performance. The flock-mates could have had prior experiences with each other since they were captured at the same sites and they were allowed visual contact with each other during the acclimation and training periods. The cages of each flock were arranged in a way that the focal individual's cage was surrounded by the 4 cages of its flock-mates (Figure V.3). Due to test room arrangement, two of the flock-mates' cages were further from the door through which the experimenters got about (we assumed this was "safe" position for the birds) and two cages were closer to the door (considered as “risky” position); flock-mates’ cages were moved into different, randomly selected positions 3 times over the 7 sessions. The focal individual was visually separated from the 4 flock-mates except for the duration of manipulation sessions (see below). The two simultaneously manipulated flocks were visually separated from each other by opaque sheets. During the manipulation we used 16 such flocks (i.e. 8 pairs of flocks) in total.

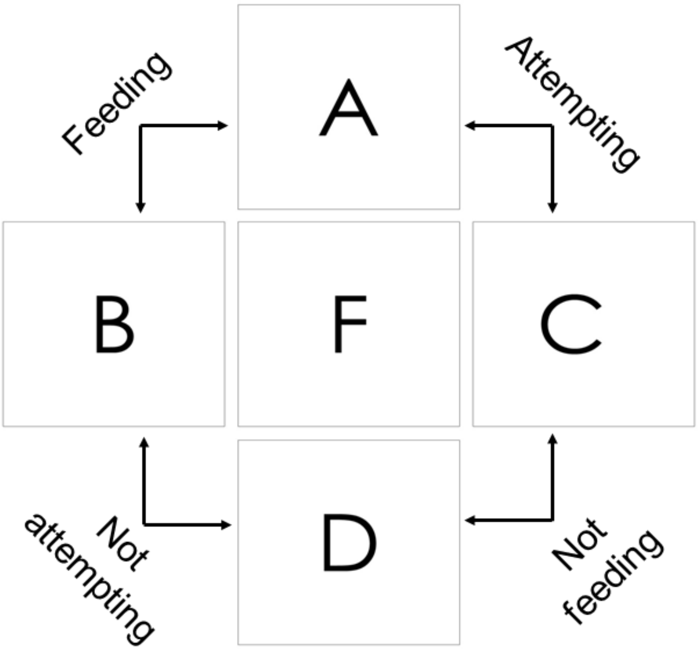

Figure V.3: An example of cage arrangement during the sessions of manipulating apparent problem-solving performance. Letters designate treatment groups as follows: F – focal individual; A – had to “problem solve” repeatedly to get food; B – received an open feeder; C – received a sealed feeder; D – had no feeder (see Methods). Note that cages of treatment groups A-D were relocated randomly 3 times over the 7 manipulation sessions.

In each flock of 5 birds, each of the 4 flock-mates was assigned to a treatment group (A-D) and during the manipulation sessions the birds of different treatment groups were presented with different feeders as follows. Birds in treatment group A were presented with the familiar training feeder, so they could solve the problem (open up the lid) repeatedly to get food during the manipulation sessions. Birds in treatment group B received an open feeder that was a training feeder with a narrow opening cut into its otherwise sealed lid, so the birds could feed without problem-solving. Birds in treatment group C received a sealed training feeder that was impossible to open, whereas birds in treatment group D and the focal individuals had no feeder in their cage during the manipulation sessions. Thus, birds in treatment groups A and B could feed during the manipulation sessions but only the former were actually problem-solving, whereas birds in treatment groups C and D were not feeding but only the former were attempting to feed by manipulating the feeder (Figure V.3). We used this 2×2 treatment design to separate the possible effect of feeding success from the effect of problem-solving success, as it is yet unclear whether sparrows may judge each other's performance by the act or the result of innovation (i.e. successful problem-solving vs. successful feeding). Birds were randomly selected for treatment groups A and C from those individuals that had been successful during training, whereas both successful and unsuccessful birds were randomly allocated to treatment groups B and D, due to the constraint that some flock-mates did not learn to open the feeder. Over the whole experiment, 5 unsuccessful birds were allocated to treatment groups B or D in 3 out of 15 flocks; omitting these 3 flocks from the analyses does not change our results qualitatively. Otherwise the treatment groups did not vary significantly in any investigated trait (Table V.1).

Table V.1: Characteristics of the focal individuals (F) and birds in the treatment groups (A-D). Mean ± SE, χ^2 and p values are shown from analysis of deviance tables of LME models with treatment group as fixed factor and flock ID as random factor (n = 15 flocks).

	Treatment groups						
	F	A	B	C	D		
Dependent variable	(*n* = 15)	(*n* = 15)	(*n* = 14)	(*n* = 15)	(*n* = 14)	χ^2	p
Innovation rank	48.72±4.68	51.3±5.1	51.1±4.7	51.6±4.4	46.3±3.4	1.32	0.858
Body mass index (g)	24.46±0.45	24.3±0.5	24.8±0.6	25.1±0.4	25.0±0.5	2.21	0.696
Aggressiveness (%)	23.36±2.88	24.5±0.0	15.0±0.0	20.6±0.0	18.8±0.1	3.73	0.444

Each manipulation session was preceded by a 60 minutes fasting period, after which the visual separation between the focal individuals and their flock-mates was suspended and birds in treatment groups A, B and C received their respective feeders for a 30 minutes session. During these sessions we observed the birds from behind a one-way window, and each minute we recorded whether each flock-mate was feeding (treatment groups A and B) or attempting to feed (i.e. touching the feeder with the beak without eating; treatment groups A and C). We chose to conduct 7 manipulation sessions because our pilot study indicated that trained birds would readily and repeatedly use the feeder, providing ample opportunity for the focal birds to observe their flock-mates' performance over a total of 3.5 hours; and our earlier experience with sparrows showed that a winter day allows sufficient time for 4 sessions per day including the fasting periods and resting time (Seress et al. 2011). On the second day we conducted 3 sessions instead of 4 to leave more time for the birds at the end of the day to accommodate to their new cage for the next stage of the experiment (see below). Apart from the manipulation sessions and the preceding fasting periods, birds had ad libitum food available from feeder dishes for focal individuals and from training feeders held open for the flock-mates.

5.2.5. Observing social interactions in flocks

After the 7th manipulation session birds were weighed and transported to the location of the social interaction observations, where each flock of those 5 birds that participated in the manipulation sessions together was housed as a flock in one of two outdoors cages (100 × 60 × 65 cm), one placed above the other. Each cage contained 3 perches, a plastic bush and 4 roosting boxes. Food, water, sand and sepia were present ad libitum except for the fasting periods before observations (see below). Food was available from a large transparent feeder box (50 × 50 × 5 cm), filled with seeds that could be obtained through 16 equidistant wells (Liker and Bókony 2009). We observed the focal birds' social interactions with their 4 flock-mates over 3 days through a one-way window as follows.

We investigated aggressive behaviours in 6 sessions (2 each day), each lasting 30 minutes. Before each session, we removed the large feeder box and all food from the cage, and birds were fasted for 60 minutes; then the flock was presented with a small feeder dish containing seeds. The feeder dish was big enough for the whole flock to feed together, and although it could be monopolized by a dominant individual this was rarely observed over the whole time of the experiment. We recorded all aggressive interactions between any two birds, noting the identity of both participants, the attacker, and the winner of the dyadic fight; we also scored the intensity of the fight on a scale from 1 to 4 (Tóth et al. 2009c) as 1—supplant: intentional movement without physical contact; 2—threat: wing display or beak gaping without physical contact; 3— peck: short physical contact; 4—fight: prolonged physical contact. Some additional aggressive interactions were recorded during the observations of spatial associations (see below).

Spatial associations of the focal individual with its flock-mates were recorded in 6 sessions (2 each day). Each session lasted for 30 minutes, during which we recorded the identity of the flock-mate nearest to the focal individual every 30 seconds, to estimate the proportion of time spent by the focal individual nearest to each flock-mate. This yielded 360 records in total for each focal individual. During the first 4 sessions, birds were not fasted and were allowed to feed freely from the large feeder box, whereas the last 2 sessions were preceded by 60 min fasting and birds could not access the food provided for these sessions; however, we obtained the same results when we analysed these two datasets separately, therefore we present results from the pooled dataset.

5.2.6. Statistical analyses

We used three dependent variables to describe the focal individuals' behaviours towards their flock-mates: (1) relative attack frequency, i.e. percentage of focal individual's attacks against the respective flock-mate out of the focal individual's all attacks; (2) attack intensity, i.e. the average intensity of focal individual's attacks against the respective flock-mate; and (3) relative association frequency, i.e. the percentage of records in which the respective flock-mate was the nearest individual to the focal bird (excluding records when more than one bird was closest to the focal individual).

To investigate whether problem-solving success of flock-mates as well as other factors (see below) affected the focal individuals' behaviours towards the flock-mates, we used linear mixed-effects (LME) models with the flock ID as random factor throughout the analyses (Pinheiro et al. 2016). Due to the death of birds B and C in one flock, we could use the data of 15 out of 16 flocks. Two further flocks were incomplete because of one bird died in each (birds B and D respectively), but omitting these flocks from the analyses did not change our results qualitatively. Initial models for each dependent variable included treatment group (i.e. the flock-mate's treatment during the manipulation sessions, A-D) as a fixed factor, and the actual innovation rank of the flock-mate and of the focal individual as covariates. Additionally, we included the following potentially confounding variables: body mass index and aggressiveness of the flock-mates, sex of the flock, date of capture, position of outdoor cages (upper or lower), and colour marking of the head of the birds. Body mass index was calculated as a measure of body condition following Peig & Green (2009), applying the equation of Bókony et al. (2012b) to the body mass data taken after the last manipulation session. Aggressiveness was calculated as the percentage of fights initiated by the respective individual out of all fights within the flock. Because the variance in mean attack intensity decreased with increasing number of attacks by the focal individual (i.e. birds that were attacked more frequently were less likely to receive extremely low or high mean intensity), we allowed for this heteroscedasticity in all models of attack intensity by using fixed variance weights. Non-significant predictors were omitted stepwise, removing the variable associated with the largest p-value in each step. We report the final models with significant effects only ($p < 0.05$) excepting that we always retained actual innovation rank in each final model to estimate its effect even if this was non-significant.

We tested whether the distribution of the focal individuals' spatial associations across its 4 flock-mates differed from random (i.e. from uniform distribution) by using χ^2 tests in each of the 15 flocks. All analyses were carried out in R 2.15.0 (R Development Core Team 2012). Mean values with ± SE and two-tailed p-values are reported.

5.3. Results

Birds behaved according to their assigned treatment (A-D) during the manipulation sessions: out of 210 records over the 7 sessions, birds in treatment group A (who had to open the feeder) were feeding or attempting to feed 80.9 ± 6.2 times, birds in treatment group B (with permanently open feeder) were feeding 85.9 ± 6.7 times, whereas birds in treatment group C (with permanently closed feeder) attempted to feed 42.3 ± 6.0 times. The frequency of interacting with the feeder (i.e. either feeding or attempting) in treatment groups A, B and C tended to increase with the individual's actual innovation rank, but only in the "safer" cage positions (Table V.2, Figure V.4). There was no difference among the 5 groups of birds (treatment groups A-D, and focal individuals) in actual innovation rank, body mass index, and aggressiveness (Table V.1).

Table V.2: The effects of cage position and innovation rank on the frequency of interacting with the feeder (either feeding or attempting to feed) during manipulation sessions in treatment groups A, B and C combined (n = 44 birds, LME with flock ID as random factor, n = 15 flocks).

Predictor variables	*b* ± SE	*t*	df	*p*
Intercept (safe position, lowest rank)	6.84 ± 2.21	3.10	26	0.002
Innovation rank	0.08 ± 0.03	1.85	26	0.071
Cage position (risky compared to safer)	2.38 ± 1.68	1.42	26	0.158
Innovation rank × cage position	-0.07 ± 0.03	-2.30	26	0.022

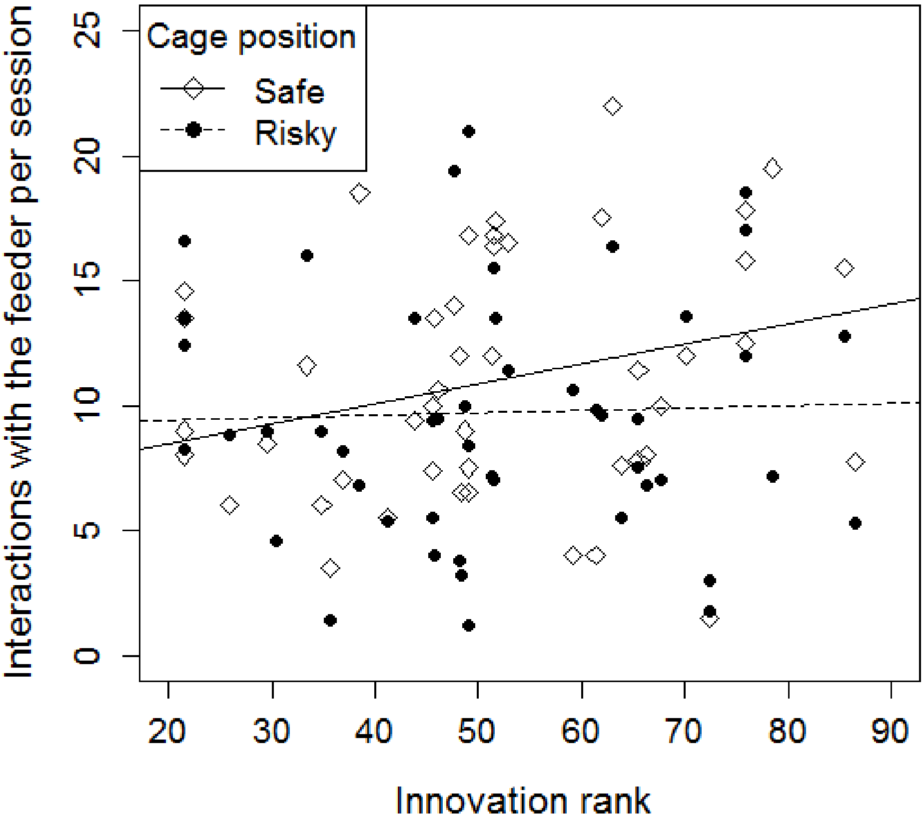

Figure V.4: Birds with higher actual innovation rank interacted with the feeder (i.e. fed or attempted to feed) more frequently when their cage was in safer position, whereas birds with lower actual innovation rank interacted with the feeder relatively infrequently in both safe and risky positions. Only birds in treatment groups A, B and C are shown as birds in treatment group D had no feeder during manipulation sessions.

We recorded 211.1 ± 19.0 aggressive interactions per flock (n = 15 flocks). Out of these the focal individuals (who had no prior social interactions with the other 4 flock-mates) participated in 98.7 ± 11.9 interactions (46.4 ± 3.1% of all fights) that tends to be higher than expected by chance (40%, one-sample t-test: $t_{14} = 2.07$, $p = 0.058$). Out of all aggressions participated in, focal individuals initiated 48.2 ± 4.0%. The focal individuals' relative attack frequency and intensity did not differ between the 4 flock-mates with different problem-solving treatments (Table V.3). The focal birds' associations were non-randomly distributed across the four flock-mates in 87% of the flocks (χ^2 tests, $p < 0.05$ in 13 out of 15 flocks) indicating that most focal birds expressed flock-mate preferences, but the treatments of flock-mates did not influence the relative association frequencies (Table V.3).

Table V.3: The focal individuals' behaviour towards the 4 treatment groups (mean ± SE). χ^2 and p values are shown from analysis of deviance tables of LME models with treatment group as fixed factor and flock ID as random factor (n = 15 flocks).

	Treatment groups					
	A	B	C	D		
Dependent variable	(*n* = 15)	(*n* = 14)	(*n* = 15)	(*n* = 14)	χ^2	*p*
Relative attack frequency (%)	28.7±5.0	21.4±2.2	29.6±4.3	23.3±3.7	3.05	0.384
Attack intensity	3.3±0.1	3.0±0.1	2.9±0.1	2.8±0.2	6.18	0.103
Relative association frequency (%)	26.3±1.6	24.0±2.5	26.7±2.2	26.4±2.3	1.03	0.795

However, the relative attack frequency of focal individuals towards their flock-mates was positively correlated with the flock-mates' actual innovation rank (Pearson correlation, r = 0.36, p = 0.005, n = 58 flock-mates), i.e. birds that had been faster innovators in the individual tests (not seen by the focal birds) were attacked more frequently by the focal individuals (Figure V.5). This relationship was robust, i.e. it remained significant after controlling for potentially confounding variables and for the non-independence of flock-mates by using mixed models (Table V.4). The focal individuals' attack intensity and relative association frequency showed no relationship with the flock-mates' actual innovation rank (Table V.4).

Table V.4: The effects of flock-mates' (n = 58) innovation rank on focal individuals' (n = 15) behaviours (dependent variables). Other predictors of the focal individuals' behavioural responses are shown only if they were retained in the final LME models (with flock ID as random factor; n = 15 flocks).

Focal individual's behaviour (dependent variable)	Flock-mate's traits (predictor variables)	*b* ± SE	*t*	df	*p*
Relative attack frequency (%)	Intercept	-75.23 ± 23.00	-3.27	40	0.002
	Innovation rank	0.43 ± 0.09	4.57	40	<0.001
	Aggressiveness (%)	0.38 ± 0.10	3.80	40	<0.001
	Body mass index	2.91 ± 0.88	3.30	40	0.002
Attack intensity	Intercept	2.17 ± 0.37	5.81	40	<0.001
	Innovation rank	0.005 ± 0.007	0.75	40	0.459
	Aggressiveness (%)	0.025 ± 0.008	3.07	40	0.004
Relative association frequency (%)	Intercept	23.63 ± 3.36	7.03	42	<0.001
	Innovation rank	0.04 ± 0.06	0.70	42	0.490

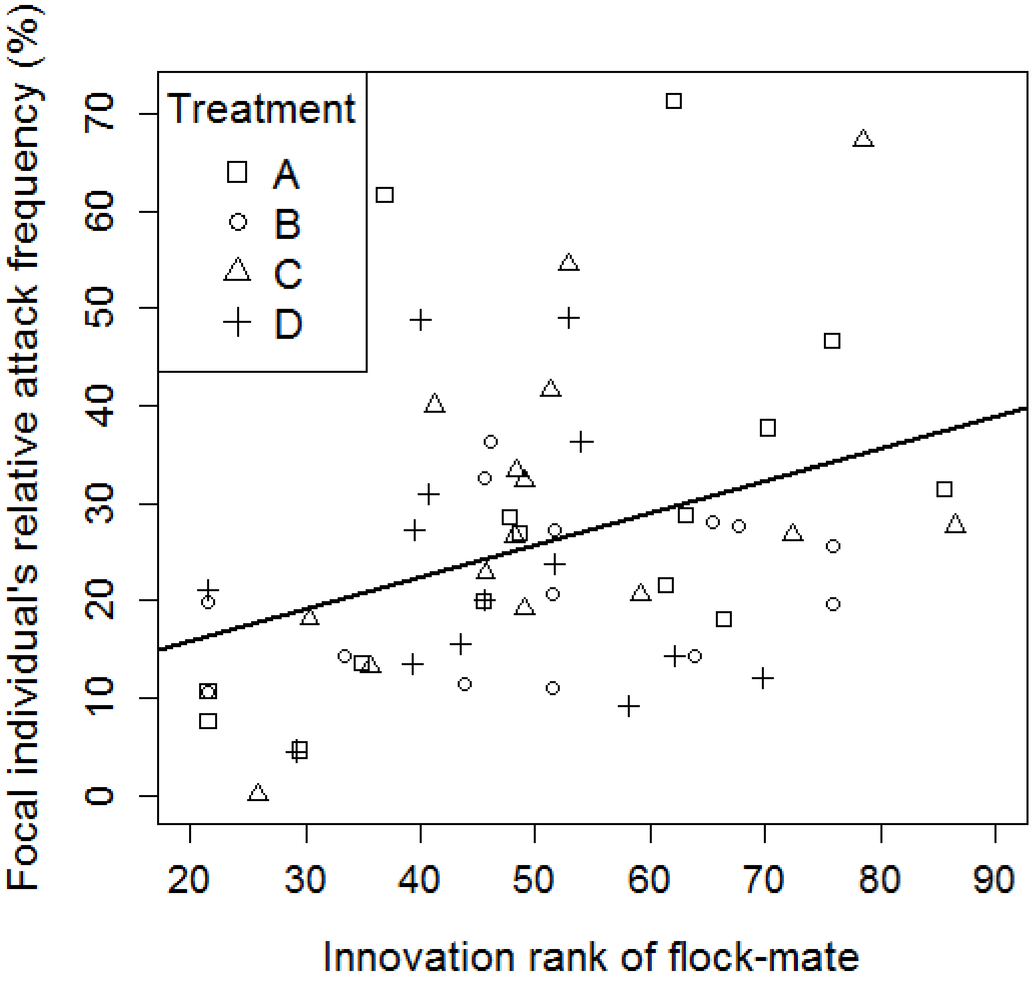

Figure V.5: Relationship between the focal individual's relative attack frequency and the flock-mates' actual innovation rank (for explanation of treatment groups see Methods and Figure V.3).

Relative attack frequency by focal individuals increased with the aggressiveness of flock-mates (r= 0.41, p= 0.001, n= 58 flock-mates; see Table V.4 for the results of mixed models), and birds with higher body mass index were also attacked more often (r= 0.33, p= 0.012, n= 58 flock-mates; Table V.4). Attack intensity of focal individuals was higher towards more aggressive flock-mates (r= 0.46, p< 0.001, n= 58 flock-mates; Table V.4). Flock-mates' actual innovation ranks did not correlate with either their aggressiveness or body mass index (Table V.5).

Table V.5: Bivariate relationships of potential confounding variables with the flock-mates' (27 males and 31 females) innovation rank and the focal individuals' (7 males and 8 females) relative attack frequency. Parameter estimates are shown from LME models, each containing a single predictor, with flock ID as random factor (n = 15 flocks).

Dependent variable	Predictor variables	*b* ± SE	*t*	df	*p*
Flock-mates' innovation rank	Aggressiveness	-11.13 ± 14.15	-0.79	42	0.436
	Body mass index	-1.83 ± 1.21	-1.51	42	0.138
	Fighting success[a]	-3.16 ± 9.49	-0.33	42	0.740
	Tarsus length[b]	4.45 ± 2.58	1.73	42	0.091
	Body mass (males)[c]	0.50 ± 2.54	0.20	19	0.847
	Body mass (females)[c]	0.51 ± 1.97	0.26	22	0.799
	Bib size (males)[d]	5.69 ± 4.12	1.38	18	0.185
	Wing bar (males)[e]	0.17 ± 0.27	0.61	18	0.548
Focal individuals' relative attack frequency (%)	Stress hormone level[f]	-4.12 ± 0.08	-1.21	42	0.234
	Attempt frequency[g]	-0.27 ± 3.41	-0.22	42	0.823
	Relative association frequency	-0.06 ± 0.14	-0.42	42	0.673

[a] number of wins divided by the number of aggressive interactions participated in (Bókony et al. 2006)

[b] length of left tarsus (± 0.1 mm)

[c] body mass after manipulation sessions (± 0.1 g). Sexes were tested separately as body mass predicts dominance in females only (Liker and Barta 2001)

[d] the area (cm^2) of black throat patch (Bókony et al. 2006)

[e] wing bar conspicuousness, greater values meaning larger contrast (Bókony et al. 2006)

[f] log-transformed concentration of corticosterone (pg/mg) in tail feathers (Bókony et al. 2014)

[g] mean frequency of attempting to open the feeder during the first 3 individual problem-solving tests (Bókony et al. 2014)

5.4. Discussion

In this study we tested experimentally whether birds take their flock-mates' innovative skills into account when interacting with them. Although the flock-mates' behaviour (e.g. the frequency of feeding or attempting to feed) during the manipulation sessions was consistent with the aims of the treatments, focal individuals did not show differential behavioural responses towards different treatment groups, e.g. did not attack or accompany more those birds that were experimentally allowed to perform successful problem-solving (treatment A) than those that were experimentally forced to appear completely unsuccessful (treatment C). In contrast, we found that aggressive behaviour was more frequent towards flock-mates with better actual problem-solving performance, although no such relationship was found for other behavioural variables (attack intensity, spatial association). We suggest several potential explanations for these conflicting results.

Firstly, one explanation is that, as suggested by the lack of difference between treatment groups, sparrows do not take the problem-solving ability of flock-mates into account during their social interactions, instead they base their decisions about aggression and association on other kinds of information (such as dominance rank or relatedness of the flock-mates; e.g. Liker and Barta 2001, 2002; Anderson 2006; Tóth et al. 2009b). For example, we found here that flock-mates' aggressiveness and body mass index both predicted the frequency of attacks by the focal individual, and aggressiveness also predicted attack intensity. If sparrows do not take each other's innovativeness into account, the correlation we found between the focal birds' aggression and the flock-mates' actual problem-solving success may have arisen by some confounding variables that may be related to the flock-mates' problem-solving success and at the same time can influence either the focal individuals' aggressive behaviour or the opportunities for interactions. For example, dominance may be associated with problem-solving behaviour in wild house sparrows like in some other group-living birds (e.g. Boogert et al. 2006, 2008), and the dominance rank of birds before the experiment (i.e. in their wild flocks) also might have had an effect on their aggressive interactions in our experimental flocks (e.g. through winner-loser effects, Rutte et al. 2006), creating a spurious correlation between aggression and problem-solving success. However, this explanation is unlikely since the actual problem-solving success of sparrows in our sample was not associated with their own fighting success in the experimental flocks, body mass and size, bib size and wing bar coloration (Table V.5), traits that have been found to predict dominance in house sparrow flocks (Møller 1987; Liker and Barta 2001; Bókony et al. 2006). Similarly, although body mass index and aggressiveness of the flock-mates correlated with the focal individuals' relative attack frequency (Table V.4), neither of these two traits was related to actual innovation rank (Table V.5). A further possibility is that the stress-sensitivity of flock-mates influenced both their problem-solving success and aggressive interactions. In an earlier study we showed for these birds that individuals with lower levels of stress hormones were more successful during some individual problem-solving tests (Bókony et al. 2014). If stress tolerance allowed these birds to spend more time at the feeder dish in the flock cages compared to the individuals with higher stress hormone levels, the focal individuals could have had more opportunity to fight with them. However, the focal birds' relative attack frequencies were not related to the stress hormone levels of flock-mates (Table V.5). Finally, the flock-mates' activity level may also affect the opportunities for the focal individuals to fight with them, e.g. less active birds with slower metabolism may spend less time at the feeder (the main site of fights); and these birds might also be less successful in problem-solving e.g. by attempting less vigorously (Benson-Amram and Holekamp 2012; Sol et al. 2012; Thornton and Samson 2012). Although birds that had higher attempt frequencies were more successful in our tests (i.e. faster solvers, see Papp et al. 2015), this kind of activity was not related to the relative attack frequency by focal birds (Table V.5).

Secondly, an alternative explanation is that focal individuals assessed their flock-mates' problem-solving ability and used this information at least in their aggressive interactions (causing our correlative result), but this assessment was not based on the manipulated problem-solving performance of flock-mates (causing the lack of treatment effect). For example, there are various behavioural (e.g. neophobia, Boogert et al. 2008) and morphological (e.g. body size, Laland and Reader 1999b; plumage coloration Mateos-Gonzalez et al. 2011) correlates of problem-solving success, and these traits can potentially be used as cues to assess the flock-mates' abilities. The use of such cues in assessing conspecifics innovativeness would allow the observers to gather social information while reducing time spent on gathering information. Furthermore, such cues may even be more reliable than the direct observation of the flock-mates' performance in actual problem-solving situations, because the social context may change the individuals' innovative performance; for example, both primates and birds perform worse in the presence of conspecifics, especially dominants (Nicol and Pope 1999; Drea and Wallen 1999; Overington et al. 2009a; Griffin et al. 2013b). In our study, we found no correlation between innovativeness and phenotypic traits that may be used as such cues (Table V.5), but the frequency of interacting with the feeder during the manipulation sessions in the "safe" cages tended to correlate positively with the birds' actual problem-solving success (Figure V.4). Thus, focal birds could potentially use this kind of activity to judge the problem-solving ability of flock-mates and adjust their behaviour accordingly during their interactions later in the experimental flocks. However, if this scenario is true, it is unclear why they did not differentiate between the treatment groups because, for example, birds in treatment group A (successful birds) had twice as many interactions with the feeder during the manipulation sessions as birds in treatment group C (unsuccessful birds; see Results). We might speculate that, instead of overall activity (i.e. interacting with the feeder), the flexibility of the flock-mates' behaviour could have served as a cue for focal individuals, as sparrows with high innovation ranks were the ones that were more active in safety than in risky cages. Interestingly, behavioural flexibility in response to predation risk was found to correlate with explorativeness in great tits (Quinn et al. 2012), and this personality trait may be a major determinant of problem-solving success (Boogert et al. 2008; Cole et al. 2012).

Regardless of the interpretation of the results, the focal individuals' behaviours clearly demonstrated that house sparrows do not discriminate their more innovative flock-mates positively. Even if the birds took their flock-mates' innovative skills into account, our results suggest that dominating over an innovator would be more important than associating with it. One reason for this can be that aggressive scrounging might be preferred to social learning by foraging house sparrows. As shown for other species, the trade-off between scrounging and social learning may suppress the latter (Giraldeau and Lefebvre 1987).

In addition to the relationship with innovativeness, we found that the agonistic behaviour of the focal individuals was positively related to the flock-mates' aggressiveness and body mass index. Furthermore, flock-mate aggressiveness predicted not only the frequency but also the intensity of attacks by the focal birds. A possible explanation for the high frequency and intensity of agonistic behaviour against aggressive flock-mates is that these birds initiated a high number of fights against the unfamiliar focal individuals (e.g. when they were feeding together on the feeder dish), which in turn might have generated a large number of counterattacks by the focal birds (e.g. if they were to regain their position on the feeder). Alternatively, since both aggressiveness and body condition may indicate resource-holding potential (Hardy and Briffa 2013), our findings may suggest that house sparrows preferentially target the strongest opponents for some reason when they are in an unfamiliar flock. Attacking the most aggressive flock-mates might pay off if the focal individual has disproportionately more to gain by defeating those flock-mates. For example, when male great tits are defeated, more aggressive ("fast") birds show stronger reduction in activity than less aggressive ("slow") birds (Carere et al. 2001). If a similar phenomenon exists in sparrows, attacking the aggressive flock-mates could be a rewarding strategy when competing for limited food sources. Note however that we did not quantify the birds' actual aggressiveness in separate assays, so we do not know if our aggressive sparrows had genuinely more aggressive personalities. In our observations, the behaviour of each bird was likely affected by the behaviour of all flock-mates, so the relative aggressiveness of a given individual was likely a function of its flock-mates' behaviour. For example, aggressive interactions are more frequent between individuals of similar fighting abilities in several species (Hardy and Briffa 2013).

Attacking flock-mates with high body mass index might pay off, for example, if these individuals are less motivated to fight due to their higher levels of energy reserves. Individuals that have more to gain by winning a contest were found to be more dedicated opponents in several cases (Morrell et al. 2005). For example, house sparrows with low body condition use aggressive scrounging more often than their flock-mates with better condition (Lendvai et al. 2004). Similarly, male house finches with drab plumage coloration (indicating poor condition) are more aggressive than colourful males (McGraw et al. 2007), and male fiddler crabs (*Uca annulipes*) with regenerated claws (weaker competitors) sometimes fight harder over resources than intact males (Callander et al. 2012). However, in our study, there was no correlation between the birds' aggressiveness and their body mass index, not supporting the above idea. Similarly, relative body size and relative body condition does not affect aggressiveness in male crickets (Brown et al. 2006). Thus, whether and how body condition and aggressiveness affect the likelihood of being attacked in agonistic interactions remains to be evaluated in further studies.

In sum, our experimental results suggest that some common social interactions (aggression, spatial association) are not influenced by the apparent problem-solving ability of the group-mates in house sparrows. On the other hand, our correlative results indicate that sparrows may take into account their flock-mates' aggressiveness, body mass index, and actual problem-solving success in aggressive interactions. The correlation between flock-mates' actual innovativeness and the focal birds' aggression suggests that the animals might be able to use subtle cues to assess the problem-solving ability of their companions instead of relying on the observation of their performance in brief foraging situations. This interesting possibility requires further testing.

CHAPTER VI.

VISUAL SEPARATION AND CAPTIVE MORTALITY

Abstract

Wild animals are often held captive for research, and for certain questions individuals need to be studied in isolation. In house sparrows, a gregarious species present on all continents but Antarctica by native range or by introduction, we report unexpectedly high mortality shortly after the birds were taken into captivity for a study on individual behaviour. This mortality was almost completely eliminated by intermittently removing visual separation between birds. We also present a systematic review of literature data on housing conditions and survival of house sparrows, highlighting the deficiency of these data in most publications. We urge researchers to report mortality and its likely causes to help improve survival of captive birds.

This chapter is an unpublished manuscript: "Preiszner, B., Papp, S., Seress, G., Vincze, E., Liker, A. & Bókony, V. Let me see my fellows: Visual contact enhances survival of a wild gregarious bird in captivity".

Research on animal behaviour and physiology often requires animals to be held captive, and in some areas of research, the individuals are isolated from conspecifics (for example, in Chapter V we measured individual problem-solving success in isolation to prevent the birds from copying or learning from their conspecifics). Wild animals may suffer mortality when taken into captivity and gregarious species may be particularly vulnerable when isolated from their conspecifics (Mason 2010), because they are adapted to live in a social environment that provides anti-predatory protection and interactions helping the individuals to explore and exploit their habitat. In studies that keep wild-caught animals in temporary captivity for research, one minimum requirement for ethical acceptability is that the rate of mortality does not exceed that observed in nature. Here we report an incidental empirical finding and a literature review to highlight the scarcity of data available for planning such ethically based protocols for captive studies. We focus on house sparrows, a bird species that lives in flocks throughout the non-breeding season and is often used as research subject in various fields of research (Anderson 2006).

6.1. Mortality in full-time and part-time visual separation

We studied individual behaviours in captive house sparrows as detailed in Preiszner et al. (2015). All details of capture, handling and housing are available from papers describing different aspects of a general project that investigates causes and consequences of behavioural flexibility in birds (Bókony et al. 2014; Papp et al. 2015; Preiszner et al. 2015; Vincze et al. 2015, 2016, and ***Chapter V***), however to make it readily available for readers we recap and summarize relevant details here. We planned the housing conditions and general procedures in this experiment similarly to our earlier studies in which we observed very little mortality in captive house sparrows (e.g. Bókony et al. 2012a). We captured 110 house sparrows in 8 weekly cohorts (10–14 individuals each week). Birds were brought into 3 weeks of captivity (Figure V.1), where they were housed as follows. Between days 1-16 birds were housed individually indoors; between days 1-5 and 13-16 in 53 × 27 × 41 cm cages, for days 6-12 they were temporarily transferred to another room into 42 × 30 × 35 cm cages. In both rooms light regime was set to 10:14 L:D and all cages were equipped with two perches and a shelter, acoustic isolation of individuals was not applied. For days 17-19 birds were relocated to outdoor group cages (100 × 60 × 65 cm), which contained perches, a plastic bush and 4 roosting boxes. Apart from the duration of tests and the preceding fasting periods, we provided ad libitum food (a mixture of millet, wheat, oat, and sunflower seeds) and tap water with multivitamin droplets throughout the study, plus sand and sepia in the outdoor cages. To facilitate the birds' habituation to the isolation that was needed for later experimental phases, for the first 5 weekly cohorts (n = 68 birds) we used a housing regime in which individually caged birds were visually separated right after transferring them to captivity ("full-time separation") up until relocating them to the outdoor group cages. For these cohorts visual separation was only suspended for 7 × 30 minutes on days 15-16 for the manipulation sessions (for details see ***Chapter V***, section 5.2.4). We witnessed unexpectedly high mortality in these five cohorts: 25.0% of the individuals died, mostly within the first 4 days of captivity (Figure VI.1), even though they had ample food and water and showed no sign of disease.

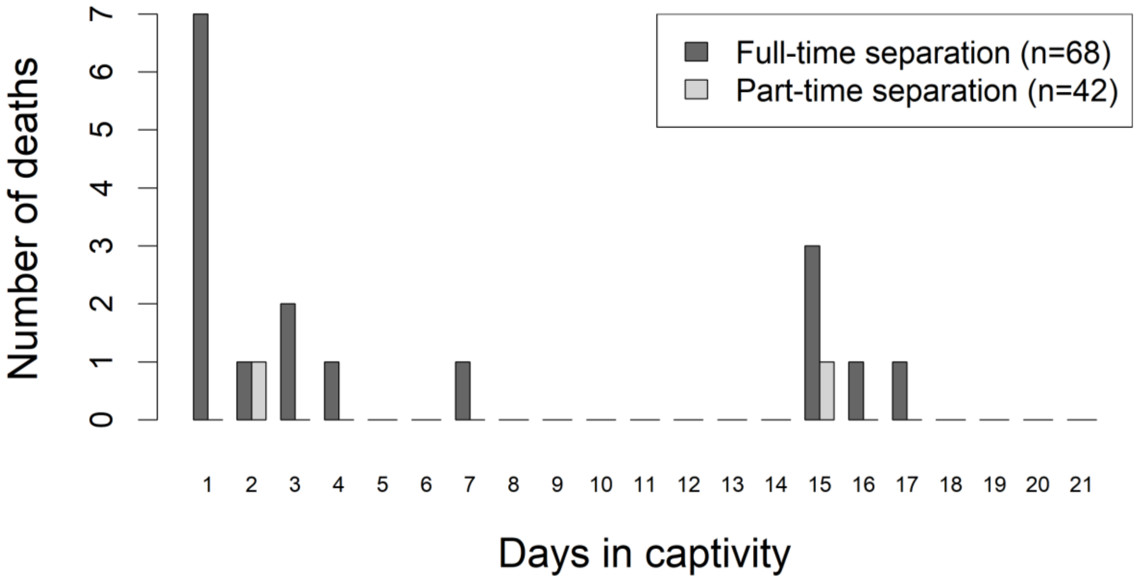

Figure VI.1: Number of deaths in relation to time spent in captivity in the two housing regimes (here day 0 as the day of capture, note that numbering of days on this figure not necessarily corresponds with Figure V.1 due to asychronous capture of birds within a cohort).

To attempt to decrease mortality we decided to change the housing regime for the last 3 cohorts ("part-time separation"). These birds (n = 42) were allowed to see their conspecifics in the neighbouring cages after capture constantly for 1-2 days, then for the next 3 days they were visually isolated only for ca. 3 hours per day (during the behavioural observations and the preceding fasting periods). For the rest of the experiment (15 days), there was no difference in the housing conditions between the first 5 and the last 3 cohorts. Using the part-time separation regime, mortality decreased to 4.8%. In total, 19 out of 110 birds died in our experiment. The majority (n=13) died during their first week after capture. A second, lower peak of mortality around the 15th day of the experiment for each cohort (Figure VI.1) coincided with the transferring of birds from individual indoor cages into outdoor group cages.

We analysed whether housing regime had significant effect on survival using Cox's proportional hazards models in R 3.5.1 (R Core Team 2018). Time until death (see Figure VI.1) was the dependent variable; birds that survived to the end of the experiment were included as censored observations. In the initial full model, we entered the following explanatory variables: housing regime (full-time or part-time separation), type of habitat the birds were captured from (urban or rural), date of capture (number of days since 1 January 2012; range: 1-65), time of the day at capture (number of minutes since 7:00 a.m.), and body condition calculated as the scaled body mass index using the formula

$$bmi = m \times \left(\frac{19}{l_{tarsus}}\right)^{1.71}$$

where

bmi = scaled body mass index,
m = body mass upon capture (to the nearest 0.1 g), and
l_{tarsus} = tarsus length (to the nearest 0.1 mm)

following Peig & Green (2009), applying the equation of Bókony et al. (2012b). Although age may influence survival, we did not test its effect because the age of house sparrows cannot be judged with certainty based on plumage or biometry at the time of the year we conducted our study (Svensson 1992). Presumably, our sample was a mixture of first-winter birds in their 2nd calendar year and older individuals.

In this full model, only the effect of housing regime was significant (Table VI.1). Furthermore, a marginally non-significant effect of habitat type indicated that urban birds had lower mortality than those captured from rural habitats (Table VI.1). We then performed a backward-stepwise selection procedure retaining only the significant ($p < 0.05$) variables in the model. The reduced model contained only the effect of housing regime (hazards ratio of death in part-time compared to full-time separation: e^b [95% CI] = 0.169 [0.039, 0.732], p = 0.0175).

Table VI.1: The full Cox's proportional hazards model of survival. Exponentially transformed parameter estimates (e^b, along with 95% confidence intervals, CI) show the proportional change of hazard ratio, i.e. the probability of death, in response to unit change of predictors.

Predictor	e^b	95% CI	*p*
Housing[a]	0.055	0.006-0.533	0.012
Habitat[b]	0.341	0.117-1.000	0.050
Body condition[c]	1.031	0.812-1.310	0.799
Capture time of day[d]	1.003	0.997-1.008	0.308
Capture date[e]	1.028	0.987-1.071	0.178

[a] Part-time compared to Full-time separation
[b] Urban compared to Rural
[c] Grams (g)
[d] Minutes from 7 a.m.
[e] Days from 1st of January

With our data, we cannot statistically separate the effect of housing regime and date. It is possible that the intrinsic rate of mortality of the sparrows decreased over the duration of the study (Simons et al. 2019). However, it is notable that in our analyses, if date of capture is retained as the only predictor in the model, it has no significant effect ($p = 0.131$) on hazards ratio of death. This remains qualitatively the same when the sample of the two regimes are tested separately ($p = 0.362$ for the full-time, and $p = 0.998$ for the part-time separation regime). Thus, if mortality decreased with date, this decrease happened abruptly at the same time as we changed the housing regime; such a coincidence seems unlikely.

Although our experiment was not designed to test the effect of visual separation on mortality, our findings indicate that visual contact with conspecifics might be important for the wellbeing of house sparrows in the early days of captivity. While the same species fared well in similar studies when visual separation was applied after prolonged habituation to captivity in groups (Seress et al. 2011; Bókony et al. 2012a), in our full-time separation regime visual separation was applied right after introducing the birds into individual cages. Four of the birds that deceased during their first week were dissected to identify the cause of death, revealing starvation related gastric ulcers along with empty crops in all of the examined corpses. However, all birds had *ad libitum* food throughout the study except for experimental periods. Due to various treatments, length of food-deprived periods varied between the phases of the experiments and between individuals, but did not exceed 3 hours per day during the first week, and four 1.5-hours sessions per day for the rest of the experiment (30 and 60% of daylight period, respectively, see Preiszner et al. 2015). The longest possible food deprivation was 3 continuous hours, whereas the longest possible sum of daily food deprivation was 6 hours, both in case of birds that were unsuccessful in solving the daily food-acquisitioning task. Such short periods of fasting are unlikely to cause death, as mean fasting endurance under comparable captive conditions for American tree sparrows (*Spizelloides arborea*) and white-crowned sparrows (*Zonotrichia leucophrys*), both similar in size, physiology and behaviour to house sparrows, were 30.0 and 38.6 hours, respectively (Ketterson and King 1977; Stuebe and Ketterson 1982). Thus, our results suggest that getting into captivity combined with visual isolation from social companions may cause overwhelming stress to house sparrows, which results in food negligence and starvation to death, but can be alleviated by ensuring visual contact with conspecifics. Since Stuebe & Ketterson (1982) found weight loss and decreased food intake in visually separated American Tree Sparrows, our findings may also apply for other gregarious species.

6.2. Systematic review of mortality in captive house sparrows

To assess if survival rate witnessed in captivity is acceptable, we can compare the mortality rates observed in captivity to those measured in nature. Free-living house sparrows' annual mortality rates (Anderson 2006) range between 0.17-0.69 (median = 0.45; mean ± SE = 0.44 ± 0.04, n = 11 studies) for adults, and 0.42-0.92 (median = 0.68; mean ± SE = 0.67 ± 0.08, n = 5 studies) for juveniles. For a period of 20 days (i.e. the mean of the number of captive days in our experiment), these values translate into a mean of 3 and 6% mortality for the two age groups, respectively (see calculation below). As our sample consisted of unknown proportions of adults and juveniles, it appears acceptable that mortality of the birds in our part-time separation regime (4.8%) fell between the means of free-living adults and juveniles. In contrast, the mortality in our full-time separation regime (25.0%) was 4-8 times higher than the natural rates. To answer the question to what extent this variability may be explained by visual separation, we conducted a systematic review of captive studies on house sparrows. Specifically we were interested in the occurrence of visual separation and its potential effects on mortality patterns, therefore we reviewed 108 studies and we extracted data on mortality and housing.

We performed a literature search in the Scopus database on the 12th of December 2018 using the search string: "TITLE-ABS-KEY (passer OR sparrow) AND TITLE-ABS-KEY (captive OR captivity OR captive-bred)" resulting in 259 documents. On the same day we also performed a search in the Web of Science database using the string: "TS=(passer OR sparrow) AND TS=(captive OR captivity OR captive-bred)” resulting 535 documents. After combining the two results and removing the duplicates 584 records remained. Then, we filtered the titles to exclude papers concerning other species; 257 records remained. In the next step we clarified the relevance of records by reading the abstracts or full texts. We defined relevant studies as those using house sparrows in temporary or permanent captivity as model organisms, regardless of the field of research; therefore we removed papers dealing with other species or free-living house sparrows. We did not attempt to review grey literature reports. Further 12 relevant articles were added manually according to suggestions from experts of the field. During the review process, we omitted papers, which were redundant in terms of describing a different aspect of a sample of birds already represented by a record in our database. On the other hand, 5 duplicate records were added in case of papers describing studies on subsamples with different grouping or housing. This procedure resulted in a total of 103 papers representing 108 reviewed studies. We extracted data on mortality by skimming and/or searching for terms *die*, dea*, surviv*, mortal*, releas**, where “*” was used as a wild card character to be read as any number of literal characters or an empty string. We looked primarily for explicitly stated mortality rates or reported deaths along with sample sizes, and for length of captivity. In a number of cases, these data were not explicitly reported but could only be inferred indirectly (e.g. extracted from sample sizes or vague indications such as "all birds were released after the experiment" in the text). In the case of 11 studies death of birds was a planned part of the experiment, either through euthanasia for tissue sampling, or due to chemical agents tested for toxicity. In latter case, we included only those birds of the control groups. We also skimmed the papers for housing conditions (i.e. presence/absence of visual separation, group size, indoor/outdoor housing) as well as other sample properties like age, sex, geographical region, and the aims of the study. One or more of these data were not available for many of the reviewed studies (Table VI.2).

Table VI.2: Data availability (including indirect data on mortality) of sample properties in the reviewed studies (n = 108 studies).

Data type	Mortality	Study length	Age	Sex	Sample size	Indoor / outdoor	Group size
Percent available (%)	47.7	92.7	74.3	86.2	98.2	92.7	89.0

We found that only 32.4% of the reviewed studies reported mortality directly, a further 14.8% could be inferred based on sample sizes or on unclear indications of death occurrence, resulting in 51 studies with mortality data (Table VI.3). Unclear indications of death occurrence meant predominantly cases where presumably no mortality was experienced; e.g. statements such as “all birds were released to the wild” (Kimball 1996). We found 25.5% of the available data on mortality uncertain (e.g. Belmaker et al. 2012 reports mortality but never recovered the corpses, so birds might have escaped), a further 27.5% is likely to be affected by treatment or housing conditions (e.g. Nemeth et al. 2010 infected a subset with a pathogen). Omitting the data that we deemed uncertain or possibly affected by treatment, only 22.2% of the reviewed studies contained relevant and presumably reliable mortality data. A remarkably high percentage (52.3%) of the reviewed studies did not provide any data on the survival of their study subjects. In addition, many papers lack further important explicit information (e.g. length of captivity, age and sex distribution) needed to evaluate mortality relative to natural rates. Most of the reported mortality data lack comparison with previously published information, and seldom take time in captivity into account (but see e.g. Mutzel et al. 2011). Because mortality rates were reported for very different lengths of time (2 days to 2.5 years), we used the following approach to compare them to natural mortality. From the mean annual mortality rates of adult and juvenile house sparrows in the wild (Anderson 2006) we calculated their daily survival rates to be 99.84% and 99.7%, respectively as follows:

$$D = \sqrt[365.25]{S}$$

where

D = daily survival rate, and

S = mean annual survival of the respective age class in the wild

To make calculation of daily rates possible we assumed mortality to be constant over time (although natural mortality varies throughout the year, the captive studies were done with different timing and duration; we are not aware of mortality data for comparable time windows in nature). Then, for each captive study, to compare the observed mortality rates with those expected for the duration of captivity based on the average mortality rates in free-living house sparrows, we used the following equation to calculate the expected rate of mortality for each case:

$$M = 1 - (D)^t$$

where

M = expected mortality rate for the study period,
D = daily survival rate, and
t = length of study period (i.e. length of captivity, in days).

Comparing the expected and observed mortality rates (Table VI.3) we found that the majority (70.6%) of captive studies experienced lower mortality compared to natural populations. Within the studies where data on mortality were available, the proportion of birds that died (i.e. regardless of the timespan of the study) varied between 0.00-0.77 (median = 0.07; mean ± SE = 0.12 ± 0.02). Omitting those studies where the treatment was likely to affect mortality (e.g. corticosterone treatment), and those where the mortality estimation was uncertain (e.g. mortality was reported but corpses were never recovered) resulted in 24 studies with proportion of birds that died between 0.00-0.32 (median = 0.07, mean ± SE 0.09 ± 0.02, Table VI.3).

There was not enough data available in the literature to formally compare the mortality of captive house sparrows with and without visual contact. In 73.9% of the studies with individual housing, we did not find adequate information either on mortality or on the presence/absence of visual separation. Birds were housed individually for the entire time in 15 studies, of which 3 reportedly used visual separation (and two did not, while 10 did not include information regarding visual separation), but only one of these provided mortality data: Gao et al. (2017) experienced 5 times higher mortality than expected by natural rates, similarly to our full-time separation regime. Out of the 8 studies where all or a subsample of birds were only temporarily kept individually, three used visual separation (4 did not, and one did not include information regarding visual separation), out of which only two reported mortality data, as follows. In Lendvai et al. (2004) all mortality occurred before visual separation and corresponded to natural rates, whereas Bókony et al. (2010) experienced more than 4 times lower mortality than expected by natural rates; note that neither of these studies applied visual isolation at the start of captivity.

Altogether, our review has revealed a troubling dearth of published information related to the rates of mortality experienced by captive house sparrows. In the reviewed 108 studies (see full list at the end of Appendix A/III, Supplementary Material to ***Chapter VI***), where house sparrows were held captive for experimental reasons, reported mortality data proved rather sporadic and many times obscure. The studies also showed a high variation in clarity of reporting housing conditions, study length, and the characteristics of the study population, such as sex or age structure, which would be necessary for evaluating mortality. The lack of data rendered any meta-analysis of mortality patterns of visually separated and not separated house sparrows impossible. Nevertheless, the very few data available in the literature, combined with the mortality pattern found in our experiment, emphasize the importance of ample visual contact for the survival of wild-caught birds, especially in the early stages of captivity. We suspect that these findings are relevant not only for house sparrows but also for other gregarious species. We encourage researchers working with captive animals captured from the wild to report more detailed survival data of their study subjects, to facilitate comparisons among housing and experimental protocols and, ultimately, to help planning ethically acceptable studies and avoiding preventable mortality.

Table VI.3. Literature data on captive house sparrows' mortality. Of the 108 reviewed studies, here only studies with reliable mortality data are presented.

Mortality rate[a]	Observed mortality[b]	Expected mortality[c]	Sample size	Length of captivity	Group size	Visual separation	Study[d]
0.00	0	0.0	14	2 days	1	NA[e]	Lendvai & Chastel 2008
0.00	0	0.4	16	10 days	8	no	Stafford & Best 1998
0.00	0	0.6	58	5 days	2	no	Lattin et al. 2012
0.00	0	2.5	46	2-8 weeks	min. 2	no	Lattin & Romero 2014
0.00	0	7.0	129	35 days	31-34	no	Pap et al. 2010
0.02	1	9.6	59	16 weeks	14-15	no	Pap et al. 2011
0.10	2	0.4	20	min. 12 days	1	yes	Gao et al. 2017
0.10	2	0.4	20	2 weeks	2	no	Lattin et al. 2017
0.02	2	3.4	120	captive-born	12	no	Tóth et al. 2014
0.05	2	10.3	42	177 days	21	no	Vágási et al. 2018
0.04	4	2.2	100	10 days	10	no	Stafford & Best 1997
0.05	4	4.0	88	3 weeks	1 or 22	temporary	Lendvai et al. 2004
0.08	4	4.7	51	2 months	6-7	no	Gonzalez et al. 2002
0.07	4	5.4	56	1-2 months	24-32	no	Liker & Bókony 2009
0.25	4	7.0	16	12 months	16	no	Trivedi et al. 2006
0.07	4	17.2	60	5 months	1 or 14-16	temporary	Bókony et al. 2010
0.08	4	29.8	51	13 months	51	no	Moreno-Rueda & Soler 2002
0.07	4	30.9	60	65 weeks	15	no	Pap et al. 2014
0.05	7	3.0	135	10 days	15	no	Stafford et al. 1996
0.18	7	27.4	40	2 years	10	no	Seress et al. 2012
0.17	10	10.6	58	3 months	14-15	no	Seress et al. 2011
0.18	17	44.7	96	13 months	96	no	Moreno-Rueda 2010
0.19	22	10.1	114	6 weeks	3-5	no	Salleh Hudin et al. 2016
0.32	60	113.9	188	captive-born	10-15	no	Lukasch et al. 2017

[a] calculated as observed number of deaths divided by sample size

[b] number of birds that died throughout the study

[c] number of birds that would be expected to die during the study period if natural mortality rate would apply to the sample

[d] for full list of references of reviewed papers see Appendix A/III, Supplementary Material to ***Chapter VI***

[e] NA: data not available

CHAPTER VII.

GENERAL DISCUSSION

Throughout my PhD work, I studied fitness consequences and social effects of innovative behaviour in two urbanized songbird species, the great tit and the house sparrow, respectively. In this chapter, I summarize the main findings and conclusions of the work, and make suggestions for potential directions of future studies.

In free-living great tit populations, I measured innovativeness in two different tasks, and I tested whether this performance is related to various proxies of fitness in the studies presented in ***Chapters III and IV***. I demonstrated a positive correlation between problem-solving performance and breeding success in ***Chapter III***. Pairs that solved an obstacle-removal task faster had higher hatching success and higher number of fledglings. This relationship is likely to be driven by the females' performance. I also tested another proxy of fitness, the extra-pair fertilization (although the nature of its link to fitness is controversial, see Forstmeier et al. 2014). I found a positive association between females' success in the obstacle-removal task and the occurrence of extra-pair offspring in their broods, as detailed in ***Chapter IV***. Furthermore, I found that pairs of two highly neophobic individuals were less likely to have extra-pair offspring in their broods. At the same time, I found no correlation of extra-pair offspring occurrence neither with female performance in the food-acquisitioning task nor with the social father's problem-solving success in either task. Although individual problem-solving performance was not consistent across tasks, I found that urban females performed better in both tasks than their forest-dwelling conspecifics. These positive associations between innovativeness and various measures of breeding success, however context dependent they are, imply that selection favours innovative behaviour.

Although with these correlative data I cannot disentangle causality, recent evidence suggests that the positive correlation between problem-solving performance and breeding success is primarily driven by the innovativeness in great tits. In brood size manipulation experiments Cauchard et al. (2017) found that it is innovativeness that enables higher breeding success through higher provisioning rate. My results of the link between innovativeness and fitness proxies partially support earlier findings (Cole et al. 2012; Cauchard et al. 2013) corroborating that this relationship is very complex. Association between innovativeness and breeding success is robust in some aspects, whereas it is less uniform in others. For example, success in obstacle-removal tasks was found to predict nestling survival (Cauchard et al. 2013), hatching success, number of fledglings (***Chapter III***), and occurrence of extra-pair offspring (***Chapter IV***), while success in a foraging task lacked any correlation with breeding success, and promiscuity (***Chapters III*** and ***IV***, respectively) but success in a different food-acquisitioning task predicted larger clutches (Cole et al. 2012). This equivocality suggests that the variation in innovativeness can shape or can be shaped by many contrasting effects of fitness elements (e.g. higher number of offspring may be countereffected by their lower survival, as recently has been shown by Johnson-Ulrich et al. 2019) and need further exploration. For example, complexity of urban habitats make them challenging and animals seem to respond to these challenges with innovativeness. In this work, I demonstrated a positive association of female innovativeness with breeding success (hatching success, number of fledglings, and occurrence of extra-pair offspring) and with urbanization. Corroborating my results and our earlier findings recent studies found innovativeness to be generally more expressed in urban habitats (see e.g. Cook et al. 2017; Griffin et al. 2017; Kozlovsky et al. 2017). Although these results together may imply a stronger selection towards better problem-solving skills in urban environment, I found no interaction between the effects of habitat and problem-solving performance on breeding success. This latter result suggests that instead of short-term reproductive benefits (which were measured in my study) of innovativeness, other unknown benefits or reduced costs are probable mechanisms of selection for innovativeness in urban environments. For example, spatial cognitive performance was recently found to predict survival in mountain chickadees (*Poecile gambeli*, Sonnenberg et al. 2019) and more innovative parents' offspring have higher survival in house sparrows (Wetzel 2017). To find the causes/consequences of higher propensity to innovate in urban habitats future research could aim to reveal for example survival consequences of innovativeness and its variation along the urban gradient. If for example, innovativeness affects survival more positively in urban populations, it may cause an urban gradient in lifetime reproductive success, which in turn may account for the variation of innovativeness along this gradient. Such empirical studies on the fitness consequences of variation in innovativeness could be carried out ideally at study sites where most of the individuals in the population are marked, and their long-term occurrence data can be recorded. However important innovativeness may be in coping with urban habitats, it is likely that there is a wider suite of traits (Kozlovsky et al. 2017) of which different species "select" their characteristic "tool set" to succeed in anthropogenic environment (Sol et al. 2013). For example, although innovativeness did not correlate with neophobia in my studies, it is possible that, in accordance with the genetic correlation hypothesis (Forstmeier et al. 2014), a yet unknown pleiotropic relationship links such individual traits. To investigate this, a meta-analysis of general context dependency of innovativeness along with further correlative and experimental studies are needed to disentangle the links between cognitive traits, personality, innovativeness, and fitness.

In ***Chapter V***, I tested some implications of innovativeness on social interactions of captive house sparrows by measuring actual, and manipulating apparent problem-solving success in foraging tasks. I found that although more innovative individuals were attacked more frequently by their flock-mates, apparent problem-solving success did not correlate with aggressive interactions. Furthermore, although I detected social preference between flock-mates, this correlated neither with actual nor with apparent problem-solving success. These findings suggest that aggressive scrounging from innovators is more important for house sparrows than social learning when they decide how to behave towards innovative and non-innovative flock-mates. Alternatively, other yet unknown traits of flock-mates (e.g. parasite prevalence, anti-predator behaviour, cognitive abilities) might influence social preference, and thus mask the effect of innovativeness in association decisions. Nevertheless, according to my results, house sparrows' innovativeness is correlated with their social behaviour, but it seems that they do not discriminate positively their more innovative conspecifics in the establishment and maintenance of social relationships. However, despite I aimed to disentangle causality, these results remained correlative (similarily, experimental studies are needed to explore cognition's role in social interactions, see Wascher et al. 2018), and to my knowledge, there are no newer studies investigating this relationship. Therefore, as potential avenues for future research I propose firstly the exploration of cues that might help conspecifics to assess each other's innovativeness (such correlates might be e.g. behavioural or morphological traits). Secondly, this may be followed by the manipulation of such cues along with the observation of social behaviour in order to reveal the causality of its relationship with innovativeness. Finally, it is worth noting that house sparrows live in dynamic fission-fusion groups, which may render long-term associations less important (e.g. they might not be selected for remembering their flock-mates' earlier-observed performance, but rather for assessing them by their actual state). Therefore, social consequences of innovativeness are possibly more relevant in species where individuals form more coherent groups (e.g. in certain primate species).

In ***Chapter VI***, additionally to the chapters dealing with the consequences of innovativeness, I presented a possible consequence of the experiment studying innovativeness. I carried out a post-hoc analysis of mortality patterns found in the course of the experiments with captive house sparrows. I observed a surprisingly high mortality of the study subjects and

I found that permanent visual separation applied in the early days of captivity associated positively with mortality of our wild-caught house sparrows. Therefore, I recommend researchers working with wild-caught birds to keep visual isolation at the minimum level that is required for their study. Along with this analysis, in an attempt to find data for comparison I conducted a systematic review of the mortality data accessible in the literature on captive house sparrows. I found that data on mortality and housing conditions of captive house sparrows is scantily reported in the publications, rendering comparisons difficult, which in turn hinders the efforts made for improving the welfare of the study subjects. Therefore, I concluded that a more rigorous routine in reporting such data is necessary. To achieve this goal, I urge publishers to provide guidelines on reporting practices, similarly to the ethical comments on animal care, which are now mandatory in many journals.

In sum, in this thesis I found that innovativeness is correlated to some key aspects of individual fitness, such as breeding and social interactions. In great tits, female innovativeness is positively correlated with proxies of breeding success and with the frequency of extra-pair offspring in the broods suggesting fitness consequences. Innovativeness seems to be taken into account in aggressive behaviour of house sparrows; more innovative individuals get attacked more often, possibly in order to facilitate scrounging. Therefore, this thesis furthers the knowledge on the evolution of innovativeness; it strengthens the presumed links of innovativeness and fitness and it contributes to the understanding of the role of innovativeness in social relationships. I successfully manipulated the apparent problem-solving performance of individuals in an attempt to disentangle some of the social consequences of it, and to the best of my knowledge, no other study to date applied such an experimental approach to study innovativeness. As the manipulation had no effect on house sparrows' social behaviours, my results on the fitness consequences of innovativeness remain correlative. This further emphasizes the importance of experimental studies in identifying and understanding the proximal mechanisms that shape the variation of innovative behaviour between and within populations. Innovative problem-solving and animal cognition is a current hot topic of behavioural ecology and ecology in general with implications for applied science (e.g. recent technological advances resulted in robots capable of creative problem-solving, Gizzi et al. 2019). Therefore, I expect that several novel results are coming up, some of which will help to disentangle the equivocalities in the behavioural literature in general, and answer the specific questions that arose in my thesis.

THESIS POINTS

1. I measured both problem-solving success and breeding performance of free-living great tit pairs. I found positive correlation of hatching success and the number of fledglings (proxies for breeding success) with success in an obstacle-removing task, but not with success in a food-acquisitioning task. These relationships were likely to be driven by female behaviour.
2. By measuring problem-solving success in urban and forest habitats as well, I found urban birds to be faster problem-solvers suggesting increased benefits of innovativeness in urban compared to natural habitats. However, the correlations between innovativeness and breeding success were similar in urban and forest habitats. These results imply that selection may favour innovativeness but do not support that this effect would be stronger in urban habitats. Thus, the higher innovativeness of urban birds might be due to other benefits and/or lower costs.
3. In free-living great tits, the occurrence of extra-pair offspring was more frequent in broods of females that were successful in an obstacle-removal task, which was solved almost exclusively by females, compared to the broods of unsuccessful females. Furthermore, I found no correlation between male innovativeness and the occurrence of extra-pair offspring in the males' nest. The hypothesis that the social male’s low innovativeness drives the female’s extra-pair sexual behaviour is not supported by these results. Instead, they imply that female innovativeness may facilitate the pursuit of and/or the exposure to extra-pair mating attempts.
4. I tested whether the individuals' innovativeness observed by their flock-mates affects social interactions. I found no evidence for this hypothesis by experimentally manipulating apparent problem-solving success of captive house sparrow individuals, because the frequency and intensity of aggression and the frequency of spatial associations between the flock-mates were unrelated to their apparent (manipulated) problem success.
5. I also tested whether the individuals' inherent, non-manipulated innovativeness affects their social interactions in the same house sparrows. I found that the more innovative individuals were attacked more frequently, although innovativeness was not related to the intensity of attacks by flock mates or frequency of close spatial association with flock mates. These results suggest that house sparrows may take their flock-mates’ innovativeness into account in their aggressive social behaviour, but they do not assess it through direct observation of problem solving; they rather may use some unknown indirect cues.

6. In a follow-up investigation, I found that captive house sparrows survive better during the first few days of captivity if they are not visually isolated from conspecifics. These results draw attention to the importance of visual contact for wild-caught birds during the first days of captivity, warning ornithologists to minimize visual separation to avoid a stressor potentially increasing mortality. I carried out a systematic review of the literature on captive house sparrows' mortality, and I found that most publications lack data on the mortality and housing conditions of the study objects. I urge researchers to report mortality and its likely causes to help improve the survival of captive birds.

TÉZISPONTOK

1. Vadon élő széncinege párokban mértem a szaporodási és problémamegoldási sikert. Pozitív összefüggést találtam egy akadályeltávolító feladatban elért sikeresség, valamint a fészkek kelési sikere és a kirepült fiókák száma között (mindkettővel becsülhető a szaporodási siker), azonban nem találtam ilyen kapcsolatot a táplálkozási feladatban elért sikerrel. Az összefüggések feltehetően a tojók problémamegoldási sikerén alapulnak.
2. Széncinegék problémamegoldási sikerét városi és erdei populációkban egyaránt felmérve a városi madarak jobban teljesítettek. Ez alapján arra következtethetünk, hogy az innovativitás városi környezetben magasabb haszonnal jár az erdei élőhelyhez képest. Ennek ellenére az innovatív viselkedés és a szaporodási siker közötti összefüggések hasonlóak voltak városi és erdei élőhelyen egyaránt. A fentiek azt sugallják, hogy az innovatív viselkedés előnyös a szaporodási siker szempontjából, de nem támasztják alá azt, hogy ez az előny nagyobb lenne városi környezetben. A városi egyedek sikeresebb problémamegoldását tehát más előnyök és/vagy alacsonyabb költségek magyarázhatják.
3. Egy akadályeltávolító feladatot sikeresen megoldó tojók fészekaljaiban a sikertelen tojókéhoz viszonyítva gyakrabban fordultak elő extra-pár utódok vadon élő széncinege populációkban. A hímek innovativitása és a fészekaljaikban található extra-pár utódok gyakorisága között nem találtam kapcsolatot. Ezek az eredmények nem igazolják a feltételezést, miszerint a tojók extra-pár szaporodási viselkedését befolyásolja a párjuk innovativitása. Eredményeim inkább arra engednek következtetni, hogy a tojók innovativitása elősegíti az extra-pár kapcsolatok keresését és/vagy megnöveli a páron kívüli párzásokat kereső hímeknek való kitettségüket.
4. Fogságban tartott házi verebeken vizsgáltam, hogy a csapattársak által megfigyelt, kísérletesen manipulált problémamegoldási siker befolyásolja-e a szociális viselkedést. Az eredmények nem támasztották alá, hogy a társak által megfigyelhető problémamegoldási teljesítmény szerepet játszik a társas kapcsolatokban.
5. Ugyanazon fogságban tartott házi verebek esetében viszont a valóban innovatív egyedeket gyakrabban támadták a csapattársaik, a támadások hevessége és a térbeli asszociációk gyakorisága azonban nem függött az egyed valódi (nem manipulált) innovativitásától. Ezek az eredmények arra engednek következtetni, hogy bár a házi verebek agresszív viselkedésük során figyelembe vehetik a társak innovativitását, azt nem az innovatív

viselkedés közvetlen megfigyelésével mérik fel, hanem valamilyen más, eddig ismeretlen közvetett jelzésen vagy más tulajdonságon keresztül.

6. Azt találtam, hogy fogságban tartott házi verebek túlélési valószínűsége magasabb a fogság első napjaiban, ha a fajtársaikat láthatják. Ez az eredmény felhívja a figyelmet a vizuális kontaktus fontosságára a madarak befogását követő első napokban. A kutatóknak érdemes tehát a feltétlen szükséges minimum szintre korlátozni az egyedek vizuális elkülönítését. Áttekintettem a fogságban tartott házi verebekre vonatkozó szakirodalmat, hogy felmérjem a mortalitás mértékét különböző tartási körülmények esetén. A legtöbb publikáció azonban igen hiányos volt a túlélési adatok, valamint a tartási körülmények tekintetében. A fogságban tartott madarak túlélési valószínűsége növelésének érdekében szorgalmazom, hogy a szerzők a jövőben részletesen közöljék a vizsgálatukra vonatkozó tartási körülményeket, és a vizsgálat során tapasztalt mortalitási mintázatot.

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ETHICAL COMMENTS

All procedures described in my thesis were in accordance with the guidelines for animal care outlined by ASAB/ABS and Hungarian laws, and were licensed by the Middle Transdanubian Inspectorate for Environmental Protection, Natural Protection and Water Management (permission number: 31559/ 2011).

PUBLICATIONS

Publications and manuscripts included in the thesis:

Preiszner, B., Papp, S., Seress, G., Vincze, E., Liker, A. & Bókony, V. Let me see my fellows: Visual contact enhances survival of a wild gregarious bird in captivity. **Manuscript**

Bókony, V., Pipoly, I., Szabó, K., **Preiszner, B.**, Vincze, E., Papp, S., Seress, G., Hammer, T. & Liker, A. 2017. Innovative females are more promiscuous in great tits (*Parus major*). **Behavioral Ecology** 28(2): 579–588. **[**IF: 3.347]

Preiszner, B., Papp, S., Pipoly, I., Seress, G., Vincze, E., Liker, A. & Bókony, V. 2017. Problem-solving performance and reproductive success of great tits in urban and forest habitats. **Animal Cognition** 20: 53-63. [IF: 2.805]

Preiszner, B., Papp, S., Vincze, E., Bókony, V. & Liker, A. 2015. Does innovation success influence social interactions? An experimental test in house sparrows. **Ethology** 121: 661-673. [IF: 1.717]

Publications not included in the thesis:

Boros, G., Czeglédi, I., Erős, T. & **Preiszner, B.** 2020. Scavenger-driven fish carcass decomposition and phosphorus recycling: laboratory experiments with freshwater fish and crayfish. **Freshwater Biology** DOI: 10.1111/fwb.13576.

Cech, G., Sándor, D., Molnár, K., Paulus, P., Papp, M., **Preiszner, B.**, Vitál, Z., Varga, Á. & Székely, C. 2020. New record on the metacercariae of the North American *Posthodiplostomum centrarchi* (Digenea, Diplostomidae) in pumpkinseed (*Lepomis gibbosus*) in Hungary. **Acta Veterinaria Hungarica** DOI: 10.1556/004.2020.00001.

Kralj, J., Martinović, M., Jurinović, L., Szinai, P., Sütő., S. & **Preiszner, B**. 2020. Geolocator study reveals east African migration route of Central European Common Terns. **Avian Research** 11:6.

Czeglédi, I., **Preiszner, B.**, Vitál, Z., Kern, B., Boross, N., Specziár, A., Takács, P. & Erős, T. 2019. Habitat use of invasive monkey goby (*Neogobius fluviatilis*) and pumpkinseed (*Lepomis gibbosus*) in Lake Balaton (Hungary): a comparison of electrofishing and fyke netting. **Hydrobiologia** 846(1): 147-158 [IF: 2.325]

Vincze, E., Pipoly, I., Seress, G., **Preiszner, B.**, Papp, S., Németh, B., Liker, A. & Bókony, V. 2019. Great tits take greater risk toward humans and sparrowhawks in urban habitats than in forests. **Ethology** 125:686–701. [IF: 1.525]

Pipoly, I., Szabó, K., Bókony, V., **Preiszner, B.**, Seress, G., Vincze, E., Schroeder, J. & Liker, A. 2019. Higher frequency of extra-pair offspring in urban than forest broods of great tits (*Parus major*). **Frontiers in Ecology and Evolution** 7:229. [IF: 2.686]

Takács, P., Ács, A., Bánó, B., Czeglédi, I., Csaba, J., Erős, T., Fésűs-Móré, M., **Preiszner, B.**, Staszny, Á., Vitál, Z., Weiperth, A., & Ferincz, Á. 2019. "Invasion in progress": first occurrence and spread of river nerite (*Theodoxus fluviatilis*, L. 1758) in the largest Central European shallow lake, Lake Balaton, Hungary. **BioInvasions Records** 8(2), 273-280. [IF: 1.208]

Seress, G., Hammer, T., Bókony, V., Vincze, E., **Preiszner, B.**, Pipoly, I., Sinkovics, C., Evans, K. & Liker, A. 2018. Impact of urbanization on abundance and phenology of caterpillars and consequences for breeding in an insectivorous bird. **Ecological Applications** 28: 1143-1156. [IF: 4.393]

Boross N., Czeglédi I., **Preiszner B.**, Burányi M., Boros G., Erős T., Kern B., Specziár A., Takács P. & Vitál Z. 2018. Szíjgalandféreg (*Ligula intestinalis*) fertőzés hatása a balatoni folyami gébek (*Neogobius fluviatilis*) kondíciófaktorára és ivarszerv tömegére. **Hidrológiai közlöny** 98: 15–21.

Czeglédi I., Boros G., **Preiszner B.**, Specziár A., Takács P., Vitál Z. & Erős T. 2018. Halfaunisztikai vizsgálatok a Sió-csatornán. **Pisces Hungarici** 12: 33-36.

Vitál Z., Czeglédi I., **Preiszner B.**, Specziár A., Takács P., Kern B., Erős T. & Boross N. 2018. A folyami géb (*Neogobius fluviatilis*) balatoni állományának testhosszeloszlása, szaporodásbiológiája, valamint a ligulózis hatása a gonado-szomatikus indexük értékére. **Pisces Hungarici** 12: 77-86.

Takács P., Bánó B., Czeglédi I., Ferincz Á., Kern B., Preiszner B., Staszny Á., Vitál Z., Weiperth A. & Erős T. 2018. Hány csukafaj él a Kárpát-medencében? **Pisces Hungarici**: 12: 67-70.

Seress, G., Vincze, E., Pipoly, I., Hammer, T., Papp, S., **Preiszner, B.**, Bókony, V. & Liker, A. 2017. Effects of capture and video-recording on the behavior and breeding success of Great Tits in urban and forest habitats. **Journal of Field Ornithology** 88(3): 299-312. [IF: 1.394]

Vincze, E., Papp, S., **Preiszner, B.**, Seress, G., Bókony, V. & Liker, A. 2016. Habituation to human disturbance is faster in urban than rural house sparrows. **Behavioral Ecology** 27(5): 1304-1313. [IF: 3.311]

Papp, S., Vincze, E., **Preiszner, B.**, Liker, A. & Bókony, V. 2015. A comparison of problem-solving success between urban and rural house sparrows. **Behavioral Ecology and Sociobiology** 69: 471-480. [IF: 2.382]

Vincze, E., Papp, S., **Preiszner, B.**, Seress, G., Liker, A. & Bókony, V. 2015. Does urbanization facilitate individual recognition of humans by house sparrows? **Animal Cognition** 18: 291-298. [IF: 2.161]

Bókony, V., Lendvai, Á.Z., Vágási, I.Cs., Pătraş, L., Pap, P.L., Németh, J., Vincze, E., Papp, S., **Preiszner, B.**, Seress, G. & Liker, A. 2014. Necessity or capacity? Physiological state predicts problem-solving performance in house sparrows. **Behavioral Ecology** 25: 124-135. [IF: 3.177]

Pipoly, I., **Preiszner, B.**, Seress, G., Vincze, E., Liker, A. 2014. Éghajlatváltozás erdőn, mezőn: a vadon élő állatok kutatásának tanulságai, **Iskolakultúra** 11-12: 103-114.

Preiszner, B. & Csörgő, T. 2008. Habitat preference of Sylviidae warblers in a fragmented wetland. **Acta Zoologica Academiae Scientiarum Hungaricae** 54(Suppl.): 111-122. [IF: 0.522]

Conference talks, abstracts:

Boros, G., Czeglédi, I., Erős, T. & **Preiszner, B**. 2019. The role of macroscopic scavengers in nutrient release from fish carcasses. (in Hungarian) **61st Hydrobiologist Days**, Tihany, Hungary.

Vitál, Z., Boross, N., Czeglédi, I., **Preiszner, B.**, Erős, T., Cech, G., Molnár, K., Székely, C., Sándor, D. & Takács P. 2019. Establishment of the parasite *Ligula pavlovskii* in the monkey goby population of Lake Balaton. (in Hungarian) **61st Hydrobiologist Days**, Tihany, Hungary.

Megyeri, E., Takács, P., Boross, N., Czeglédi, I., **Preiszner, B.**, Erős, T. & Vitál, Z. 2019. Effect of the parasite *Ligula pavlovskii* on the breeding of the monkey goby (*Neogobius fluviatilis*). (in Hungarian) **61st Hydrobiologist Days**, Tihany, Hungary.

Preiszner, B., Boros, G., Czeglédi, I., Kern, B., Liker, A. & Erős, T. 2019. Scavenging behaviour of black bullhead (*Ameiurus melas*). **XXI. Symposium for European Freshwater Sciences (SEFS)**, Zagreb, Croatia.

Czeglédi, I., **Preiszner, B.**, Vitál, Z., Kern, B., Boross, N., Specziár, A., Takács, P. & Erős, T. 2019. Habitat use of invasive monkey goby (*Neogobius fluviatilis*) and pumpkinseed (*Lepomis gibbosus*) in Lake Balaton (Hungary). **XXI. Symposium for European Freshwater Sciences (SEFS)**, Zagreb, Croatia.

Boross, N., Czeglédi, I., Erős, T., Megyeri, E., **Preiszner, B.**, Takács, P. & Vitál, Z. 2019. Effect of the parasite *Ligula pavlovskii* on the life history traits of the monkey goby (*Neogobius fluviatilis*), an invasive benthic fish in Lake Balaton (Hungary). **XXI. Symposium for European Freshwater Sciences (SEFS)**, Zagreb, Croatia.

Takács, P., Petes, Sz., Mészáros, D. Zs., **Preiszner, B.**, Czeglédi, I., Erős, T., Bánó, B. & Vitál Z. 2019. Morphometry of pumpkinseed and monkey goby populations of lake Balaton. (in Hungarian) **15th Hungarian Conference of Ichtyology**, Debrecen, Hungary.

Vitál, Z., Boross, N., Czeglédi, I., **Preiszner, B.**, Erős, T. & Takács P. 2019. Prevalence of the parasite *Ligula pavlovskii* in the Monkey goby population of Lake Balaton. (in Hungarian) **15th Hungarian Conference of Ichtyology**, Debrecen, Hungary.

Vincze, E., Bókony, V., Pipoly, I., Seress, G., **Preiszner, B.**, Papp, S., Németh, B. & Liker A. 2018. Responses by great tits to humans and sparrowhawk in urban and non-urban habitats: general or threat-specific risk-taking behaviour? (in Hungarian) **19th Biologist Conference**, Kolozsvár, Romania.

Bukor, B., Bókony, V., Hammer, T., Papp, S., Pipoly, I., **Preiszner, B.**, Seress, G., Sinkovics, Cs., Vincze, E. & Liker, A. 2018. Frequency of re-nesting within and between years in forest and urban great tit populatons. (in Hungarian) **19th Biologist Conference**, Kolozsvár, Romania.

Preiszner, B., Boros, G., Czeglédi, I., Kern, B., Liker, A. & Erős, T. 2018. Carcass feeding behaviour of black bullhead. (in Hungarian) **60th Hydrobiologist Days**, Tihany, Hungary.

Czeglédi, I., Preiszner, B., Vitál, Z., Kern, B., Boross, N., Specziár, A., Takács, P. & Erős T. 2018. Habitat use of monkey goby (*Neogobius fluviatilis*) and pumpkinseed (*Lepomis gibbosus*) in the littoral region of Lake Balaton. (in Hungarian) **60th Hydrobiologist Days**, Tihany, Hungary.

Boross, N., Czeglédi, I., **Preiszner, B.**, Kern, B., Erős, T., Specziár, A., Takács, P., Boros, G. & Vitál Z. 2018. Prevalence of tape worm (*Ligula intestinalis*) in monkey goby (*Neogobius fluviatilis*) and the effect of ligulosis on their gonado somatic index. (in Hungarian) **14th Hungarian Conference of Ichtyology**, Tiszafüred, Hungary.

Czeglédi, I., **Preiszner, B.**, Vitál, Z., Kern, B., Boross, N., Specziár, A., Takács, P. & Erős T. 2018. Habitat use of monkey goby (*Neogobius fluviatilis*) and pupkinseed (*Lepomis gibbosus*) in the littoral region of Lake Balaton. (in Hungarian) **14th Hungarian Conference of Ichtyology**, Tiszafüred, Hungary.

Takács, P., Bánó, B., Czeglédi, I., Ferincz, Á., Kern, B., **Preiszner, B.**, Staszny, Á., Vitál, Z., Weiperth, A. & Erős T. 2018. How many Pike (*Esox*) species live in the Carpathian Basin? (in Hungarian) **14th Hungarian Conference of Ichtyology**, Tiszafüred, Hungary.

Vitál, Z., Czeglédi, I., **Preiszner, B.**, Specziár, A., Takács, P., Kern, B., Erős, T. & Boross, N. 2018. Length-frequency and reproductive biology of monkey goby (*Neogobius fluviatilis*) in Lake Balaton. (in Hungarian) **14th Hungarian Conference of Ichtyology**, Tiszafüred, Hungary.

Vincze, E., Bókony, V., Pipoly, I., Seress, G., **Preiszner, B.**, Papp, S., Németh, B. & Liker, A. 2017. Responses by great tits to humans and sparrowhawk in urban and non-urban habitats: general or threat-specific risk-taking behaviour? (in Hungarian) **19th Congress of the Hungarian Ethological Society**, Dobogókő, Hungary.

Seress, G., Hammer, T., Bókony, V., Vincze, E., **Preiszner, B.**, Pipoly, I., Sinkovics, C., Evans, K. L. & Liker, A. 2017. Impact of urbanization on abundance and phenology of caterpillars and consequences for breeding in an insectivorous bird, **8th International Hole-Nesting Birds Conference**, Trondheim, Norway.

Boross, N., Czeglédi, I., **Preiszner, B.**, Burányi, M., Boros, G., Erős, T., Kern, B., Specziár, A., Takács, P. & Vitál, Z. 2017. The effect of tapeworm (Ligula sp.) infection on the condition factor and gonad weight of monkey goby (*Neogobius fluviatilis*) in Lake Balaton. (in Hungarian) **59th Hydrobiologist Days**, Tihany, Hungary.

Preiszner, B., Boross, N., Erős, T., Gál, B., Kern, B., Specziár, A., Vitál, Z., Weiperth, A. & Czeglédi, I. 2017. Fyke nets in monitoring benthic fish and crayfish communities of Lake Balaton. (in Hungarian) **59th Hydrobiologist Days**, Tihany, Hungary.

Pipoly, I., Bókony, V., Donald, P.F., Hammer, T., Kirkpatrick, M., Papp, S., **Preiszner, B.**, Schroeder, J., Seress, G., Szabó, K., Székely, T., Vincze, E. & Liker, A. 2016. Environmental factors affecting sex ratio and reproductive success. (in Hungarian) **18th Congress of the Hungarian Ethological Society**, Debrecen, Hungary.

Sinkovics, C., Seress, G., Pipoly, I., Hammer, T., Vincze, E., Papp, S., **Preiszner, B.** & Liker, A. 2016. Sex and habitat differences in the parental care behavior of great tits (*Parus major*). (in Hungarian) **18th Congress of the Hungarian Ethological Society**, Debrecen, Hungary.

Szabó, K., Pipoly, I., **Preiszner, B.**, Hammer, T., Papp, S, Seress, G., Vincze, E., Liker, A. & Bókony, V. 2015. Promiscuity and problem solving success of great tits (*Parus major*) (in Hungarian). **17th Congress of the Hungarian Ethological Society**, Dobogókő, Hungary.

Seress, G., Vincze, E., Hammer, T., Papp, S, Pipoly, I., **Preiszner, B.** & Liker, A. 2015. Effects of capture on the behavior and breeding success of birds in differently urbanized habitats (in Hungarian). **17th Congress of the Hungarian Ethological Society**, Dobogókő, Hungary.

Preiszner, B., Papp, S., Pipoly, I., Seress, G., Vincze, E., Liker, A. & Bókony, V. 2015. Urbanization, problem-solving and reproductive success in Great Tits Parus major. **10th Conference of the European Ornithologist's Union**, Badajoz, Spain.

Bókony, V., Lendvai, Á.Z., Vágási, I.Cs., Seress, G., Papp, S., **Preiszner, B.,** Vincze, E. & Liker, A. 2015. Measuring urbanization and its effects on avian physiology: pitfalls and approaches. **10th Conference of the European Ornithologist's Union**, Badajoz, Spain.

Preiszner, B., Vincze, E., Papp, S., Pipoly, I., Seress, G., Liker, A. & Bókony, V. 2015. Problem-solving performance and reproductive success in urban and rural great tits. **Behaviour 2015**, Cairns, Australia.

Papp, S., Vejnovic, A., Hammer, T., Vincze, E., **Preiszner, B.,** Pipoly, I., Seress, G., Bókony, V. & Liker, A. 2015. Risk taking behaviour of urban and forest dwelling great tits (*Parus major*). (in Hungarian) **10th Congress of Hungarian Ecologists**, Veszprém, Hungary.

Németh, B., Vincze, E., Papp, S., **Preiszner, B.,** Seress, G., Hammer, T., Liker, A. & Bókony, V. 2015. Behavioural responses of great tits (*Parus major*) to presence of a predator along the urbanization gradient. (in Hungarian) **10th Congress of Hungarian Ecologists**, Veszprém, Hungary.

Vincze, E., Pipoly, I., Hammer, T., Papp, S., **Preiszner, B.,** Seress, G., Németh, B., Bókony, V. & Liker, A. 2014. Behavioural responses to humans and predators by urban and rural passerines. (in Hungarian) **16th Congress of the Hungarian Ethological Society**, Tihany, Hungary.

Pipoly, I., Hammer, T.,Papp, S., **Preiszner, B.,** Seress, G., Szabó, K., Vincze, E., Bókony, V. & Liker, A. 2014. The frequency of extra-pair youngs in urban and rural Great Tit (*Parus major*) populations. (in Hungarian) **16th Congress of the Hungarian Ethological Society**, Tihany, Hungary.

Papp, S., Hammer, T., Vincze, E., **Preiszner, B.,** Pipoly, I., Seress, G., Liker, A. & Bókony, V. 2014. Effects of urbanization on neofobia and problem-solving success in house and tree sparrows. (in Hungarian) **16th Congress of the Hungarian Ethological Society**, Tihany, Hungary.

Seress, G., Papp, S., Pipoly, I., **Preiszner, B.,** Vincze, E., Liker, A. & Bókony, V. 2014. Size matters: effects of habitat urbanization on nestling provisioning of two sparrow species. (in Hungarian) **16th Congress of the Hungarian Ethological Society**, Tihany, Hungary.

Vincze, E., Papp, S., **Preiszner, B.,** Seress, G., Liker, A. & Bókony, V. 2014. Flight initiation distance and habituation to humans in urban and rural house sparrows. **"Spring Wind" Conference 2014**, Debrecen, Hungary.

Vincze, E., Papp, S., **Preiszner, B.,** Seress, G., Liker, A. & Bókony, V. 2014. Flight initiation distance and habituation to humans in urban and rural house sparrows. **7th European Conference on Behavioural Biology**, Prague, Czech Republic.

Bókony, V., Hammer, T., Papp, S., Pipoly, I., **Preiszner, B.**, Seress, G., Sinkovics, Cs., Vincze, E. & Liker, A. 2014. Why does urbanization reduce the reproductive success of great tits? (in Hungarian) **5th Symposia of Quantitative Ecology**, Tihany, Hungary.

Vincze, E., Papp, S., **Preiszner, B.**, Seress, G., Liker, A. & Bókony, V. 2013. Comparing Flight Initiation Distance and Habituation to Humans between Urban and Rural Birds. (in Hungarian) **15th Congress of the Hungarian Ethological Society**, Budapest, Hungary.

Preiszner, B., Bókony, V. & Liker, A. 2013. The role of individual problem-solving success in social status of House Sparrows (*Passer domesticus*). **Science for sustainability**, Győr, Hungary.

Bókony, V., Lendvai Á.Z., Vágási, I.Cs., Patras, L., Pap, P.L., Vincze, E., Papp, S., **Preiszner, B.**, Seress, G. & Liker, A. 2013. Necessity or capacity? Physiological state predicts problem-solving performance in house sparrows. **Behaviour 2013**, Newcastle, United Kingdom.

Preiszner, B., Bókony, V. & Liker, A. 2012. Is social status affected by individual problem-solving success in House Sparrows (*Passer domesticus*)? **14th Congress of the Hungarian Ethological Society**, Kolozsvár, Romania.

Preiszner, B., Bókony, V. & Liker, A. 2012. Is social status of House Sparrows (*Passer domesticus*) affected by individual problem-solving success? (in Hungarian) **1st Conference of Doctoral Schools of Environmental Sciences**, Budapest, Hungary.

Csörgő, T., Miholcsa, T. & **Preiszner, B.** 2007. Results of a long term monitoring scheme. (in Hungarian) **Bird Ecology Symposium** - Ecology and Conservation Section of Hungarian Biological Society, Budapest, Hungary.

Conference posters, abstracts:

Cech, G., Sándor, D., Molnár, K., Papp, M., Deák-Paulus, P., **Preiszner, B.**, Vitál, Z., Czeglédi, I., Varga, Á. & Székely, C. 2019. First observation of the North-American *Posthodiplostomum centrarchi* Hoffman, 1958 in Hungary. **19th International Conference on Diseases of Fish and Shellfish,** Porto, Portugal.

Vitál Z., Boross N., Czeglédi I., **Preiszner B.**, Erős T. & Takács P. 2019. Delayed parasite occurrence in a persistent fish invader: Prevalence of *Ligula pavlovskii* in monkey gobies (*Neogobius fluviatilis*) in Lake Balaton. **XXI. Symposium for European Freshwater Sciences (SEFS)**, Zagreb, Croatia.

Takács, P., Ács, A., Bánó, B., Czeglédi, I., Csaba, J., **Preiszner, B.**, Staszny, Á., Vitál, Z., Erős, T. & Ferincz, Á. 2018. “Invasion in progress”: first occurrence and spread of river nerite (*Theodoxus fluviatilis*) in the Lake Balaton. (in Hungarian) **60th Hydrobiologist Days**, Tihany, Hungary.

Sinkovics, C., Seress, G., Hammer, T., Pipoly, I., Papp, S., **Preiszner, B.**, Vincze, E. & Liker, A. 2016. Differences in composition and biomass of nestlings’ food between urban and forest great tits. **Student Conference on Conservation Science**, Tihany, Hungary.

Hammer, T., Papp, S., Seress, G., Pipoly, I., **Preiszner, B**., Vincze, E. & Liker, A. 2015. Effects of radio telemetry tagging on the behavior of great tits (*Parus major*) (in Hungarian). **17th Congress of the Hungarian Ethological Society**, Dobogókő, Hungary.

Seress, G., Hammer, T., Papp, S., Pipoly, I., **Preiszner, B.,** Vincze, E. & Liker, A. 2015. The effects of nest-trapping and video-recording on breeding birds' behaviour. **10th Conference of the European Ornithologist's Union,** Badajoz, Spain.

Sütő, S., Ferincz, Á., Liker, A., Szinai, P. & **Preiszner, B.** 2014. The breeding site fidelity and migration routes of Common Terns (*Sterna hirundo*) in Hungary. (in Hungarian) **56th Hungarian Hydrobiologist Days**, Tihany, Hungary.

Seress, G., Papp, S., Pipoly, I., **Preiszner, B.**, Vincze, E., Bókony, V. & Liker, A. 2014. Size matters: effects of habitat urbanization on nestling provisioning in two sparrow species. **7th European Conference on Behavioural Biology**, Prague, Czech Republic.

Hammer, T., Papp, S., Pipoly, I., **Preiszner, B.**, Seress, G., Vincze, E., Liker, A. & Bókony, V. 2014. Effects of habitat urbanization on the breeding success of Great Tits (*Parus major*) **7th European Conference on Behavioural Biology**, Prague, Czech Republic.

Preiszner, B., Papp, S., Vincze, E., Seress, G., Bókony, V. & Liker, A. 2013. Let me see my fellows!! Neighbour visibility affects survival of captive social birds. **15th Congress of the Hungarian Ethological Society**, Budapest, Hungary.

Preiszner, B., Papp, S., Vincze, E., Seress, G., Bókony, V. & Liker, A. 2013. Is Social Status Influenced by Individual Problem-Solving Success in House Sparrows (*Passer domesticus*)? **14th Congress of The European Society for Evolutionary Biology**, Lisbon, Portugal.

Papp, S., Vincze, E., **Preiszner, B.,** Seress, G., Liker, A. & Bókony, V. 2013. Problem solving success in urban and rural house sparrows *Passer domesticus*. **9th Conference of the European Ornithologists' Union**, Norwich, United Kingdom.

Vincze, E., Papp, S., **Preiszner, B.,** Seress, G., Liker, A. & Bókony, V. 2013. Recognition of individual humans differs between urban and rural house sparrows. **Behaviour 2013**, Newcastle, United Kingdom.

Preiszner, B., Bókony, V. & Liker, A. 2012. Effect of individual problem-solving success on the social status of House Sparrows (*Passer domesticus*). (in Hungarian) **9th Congress of Hungarian Ecologists**, Keszthely, Hungary.

Preiszner, B. & Csörgő, T. 2007. Effects of fragmentation on Passerines' habitat use. **6th European Ornithologists Union Conference**, Vienna, Austria.

Preiszner, B. & Csörgő, T. 2007. Effects of fragmentation on Passerines' habitat use. (in Hungarian) **3rd Symposium of Synzoology**, Budapest, Hungary.

Preiszner, B. & Csörgő, T. 2006. Habitat preference of Passerines in a fragmented wetland. **5th SIL Limnology and Waterbirds Conference**, Eger, Hungary.

APPENDICES

A/I Supplementary Material to Chapter III

Table S.III.1: Effects of neophobia, response to predation risk, and response to human disturbance on problem-solving latencies.

Model	Predictors	*b* ± SE	*Z*	*p*	e^{b} [95% CI]
Obstacle-removal task					
Pairs (*n* = 52)	Neophobia[a]	-0.00 ± 0.00	-1.10	0.270	0.999 [0.998; 1.001]
	Predation risk[b]	0.07 ± 0.74	0.10	0.921	1.076 [0.253; 4.573]
	Human disturbance[c]	1.42 ± 4.15	1.40	0.160	4.152 [0.569; 30.286]
Food-acquisition task					
Pairs (*n* = 48)	Neophobia[a]	0.00 ± 0.00	0.36	0.718	1.000 [0.999; 1.002]
	Predation risk[b]	-0.27 ± 0.63	-0.43	0.666	0.761 [0.220; 2.634]
	Human disturbance[c]	-1.86 ± 1.13	-1.64	0.101	0.156 [0.017; 1.437]

Table shows the effects of each predictor separately inserted in the initial Cox's proportional hazards models (for full description of initial models, see Chapter 3.2.2.). Positive parameter estimates (*b*) indicate positive effect on solving speed (i.e. shorter latencies). Exponentially transformed parameter estimates (e^{b}) show the proportional change of hazard ratio in response to unit change of predictors.

[a] latency to enter nestbox in neophobia test (mean values of the pair in seconds)

[b] difference in nest visit rate (visits after predator stimulus – visits after control; see methods in **Chapter III**)

[c] difference in nest visit rate (visits after human stimulus – visits before human stimulus; see methods in **Chapter III**)

Table S.III.2: Effects of the interaction between habitat type and solving latency in the obstacle-removal task on breeding success (*n* = 52 pairs).

Dependent variable	Predictor variables	*b* ± SE	*df*	*t*	*p*
Clutch size	Intercept[a]	12.005 ± 0.50	46	23.89	<0.001
	Latency[b]	-0.0003 ± 0.02	46	-0.01	0.990
	Habitat[c]	-2.665 ± 0.61	2	-4.35	0.049
	Latency × habitat[d]	-0.031 ± 0.03	46	-1.03	0.306
Hatching success	Intercept	3.806 ± 0.90	46	4.24	<0.001
	Latency	-0.040 ± 0.03	46	-1.19	0.241
	Habitat	-0.982 ± 1.01	2	-0.97	0.434
	Latency × habitat	0.001 ± 0.04	46	0.04	0.971
Number of fledglings	Intercept	11.584 ± 0.80	46	14.44	<0.001
	Latency	-0.014 ± 0.03	46	-0.51	0.611
	Habitat	-3.880 ± 1.01	2	-3.85	0.061
	Latency × habitat	-0.061 ± 0.04	46	-1.59	0.118
Proportion of chicks fledged	Intercept	0.837 ± 6.66	46	0.13	0.901
	Latency	1.763 ± 3.63	46	0.49	0.630
	Habitat	1.240 ± 6.67	2	0.19	0.870
	Latency × habitat	-1.787 ± 3.63	46	-0.49	0.625
Fledgling body mass	Intercept	18.345 ± 0.88	44	20.84	<0.001
	Latency	-0.008 ± 0.02	44	-0.34	0.738
	Habitat	-3.366 ± 0.71	2	-4.71	0.042
	Hatching date[e]	0.112 ± 0.03	44	4.20	0.000
	Trapping status[f]	-1.702 ± 0.58	44	-2.95	0.005
	Latency × habitat	-0.00006 ± 0.03	44	0.00	0.999
Fledgling tarsus length	Intercept	19.953 ± 0.30	44	67.30	<0.001
	Latency	0.012 ± 0.01	44	1.45	0.155
	Habitat	-0.505 ± 0.24	2	-2.10	0.171
	Hatching date	0.023 ± 0.01	44	2.60	0.013
	Trapping status	-0.580 ± 0.19	44	-2.98	0.005
	Latency × habitat	-0.010 ± 0.0002	44	-0.92	0.362

The table shows the results of mixed models (with study site as random factor; quasi-binomial error for hatching success and proportion of chicks fledged). The interaction term was re-inserted into the final models shown in Table III.2.

[a] mean value of the dependent variable for the fastest pairs in forests

[b] effect of problem-solving latency (min) in forests

[c] effect of habitat (urban compared to forest) in the fastest pairs

[d] difference in the effect of problem-solving latency between urban and forest habitats

[e] number of days since 1st of May

[f] at least one vs. none of the parents trapped

Table S.III.3: Effects of neophobia, response to predation risk, and response to human disturbance on breeding success (*n* = 52 pairs with valid data in the obstacle-removal test).

Dependent variable	Predictors	*b* ± SE	*df*	*t*	*p*
Clutch size	Neophobia	-0.00 ± 0.00	39	-0.60	0.554
	Predation risk	-1.33 ± 1.07	34	-1.24	0.223
	Human disturbance	1.61 ± 1.62	35	0.99	0.328
Hatching success	Neophobia	0.00 ± 0.00	39	1.28	0.207
	Predation risk	0.17 ± 1.27	34	0.13	0.898
	Human disturbance	-1.54 ± 2.35	35	-0.66	0.516
Number of fledglings	Neophobia	-0.00 ± 0.00	39	-0.22	0.830
	Predation risk	-1.25 ± 0.81	35	-1.53	0.136
	Human disturbance	-0.29 ± 2.33	35	-0.13	0.901
Proportion of chicks fledged	Neophobia	-0.00 ± 0.00	40	-0.27	0.787
	Predation risk	0.35 ± 0.64	35	0.55	0.588
	Human disturbance	0.45 ± 1.22	35	0.37	0.712
Fledgling body mass	Neophobia	0.00 ± 0.00	39	0.22	0.830
	Predation risk	-0.69 ± 1.30	34	-0.53	0.598
	Human disturbance	1.19 ± 1.98	35	0.60	0.551
Fledgling tarsus length	Neophobia	0.00 ± 0.00	39	0.87	0.390
	Predation risk	-0.16 ± 0.46	34	-0.35	0.732
	Human disturbance	-0.95 ± 0.73	35	-1.30	0.201

The table shows the effects of each predictor separately inserted in the initial mixed models (with study site as random factor; quasi-binomial error for hatching success and proportion of chicks fledged) of the respective dependent variable (for full description of initial models, see Chapter 3.2.2.).

[a] latency to enter nestbox in neophobia test (mean values of the pair in seconds)

[b] difference in nest visit rate (visits after predator stimulus – visits after control; see methods in **Chapter III**)

[c] difference in nest visit rate (visits after human stimulus – visits before human stimulus; see methods in **Chapter III**)

Table S.III.4: Effects of habitat urbanization and problem-solving latency in the food-acquisition task on breeding success (*n* = 48 pairs).

Dependent variable	Predictor variables	*b* ± SE	*df*	*t*	*p*
Clutch size	Intercept	11.85 ± 0.44	43	26.87	<0.001
	Latency[a]	0.002 ± 0.01	43	0.14	0.886
	Habitat[b]	-2.959 ± 0.42	2	-6.99	0.020
Hatching success	Intercept	3.147 ± 0.66	43	4.74	<0.001
	Latency	0.001 ± 0.02	43	0.07	0.945
	Habitat	-0.867 ± 0.62	2	-1.39	0.300
Number of fledglings	Intercept	10.38 ± 1.07	43	9.69	<0.001
	Latency	0.028 ± 0.02	43	1.44	0.158
	Habitat	-3.943 ± 1.33	2	-2.97	0.097
Proportion of chicks fledged	Intercept	4.940 ± 1.33	43	3.72	<0.001
	Latency	0.029 ± 0.02	43	1.50	0.141
	Habitat	-3.489 ± 1.39	2	-2.51	0.129
Fledgling body mass	Intercept	17.71 ± 0.97	41	18.20	<0.001
	Latency	0.011 ± 0.02	41	0.60	0.555
	Habitat	-3.172 ± 0.55	2	-5.73	0.029
	Hatching date[c]	0.111 ± 0.03	41	3.89	<0.001
	Trapping status[d]	-1.508 ± 0.68	41	-2.22	0.032
Fledgling tarsus length	Intercept	20.28 ± 0.34	41	59.75	<0.001
	Latency	-0.002 ± 0.01	41	-0.35	0.725
	Habitat	-0.777 ± 0.20	2	-3.88	0.061
	Hatching date	0.024 ± 0.01	41	2.47	0.018
	Trapping status	-0.656 ± 0.23	41	-2.80	0.008

The table shows the results of final mixed models (with study site as random factor; quasi-binomial error for hatching success and proportion of chicks fledged).

[a] problem-solving latency in minutes

[b] urban compared to forest

[c] number of days since 1st of May

[d] at least one vs. none of the parents trapped

Table S.III.5: Effects of the interaction between habitat type and solving latency in the food-acquisition task on breeding success (*n* = 48 pairs).

Dependent variable	Predictor variables	*b* ± SE	*df*	*t*	*p*
Clutch size	Intercept[a]	11.909 ± 0.58	42	20.39	<0.001
	Latency[b]	-0.0002 ± 0.02	42	-0.01	0.994
	Habitat[c]	-3.031 ± 0.69	2	-4.40	0.048
	Latency × habitat[d]	0.004 ± 0.03	42	0.13	0.895
Hatching success	Intercept	3.174 ± 0.95	42	3.34	0.002
	Latency	0.0002 ± 0.04	42	0.01	0.996
	Habitat	-0.902 ± 1.06	2	-0.85	0.485
	Latency × habitat	0.002 ± 0.05	42	0.04	0.967
Number of fledglings	Intercept	10.931 ± 1.25	42	8.76	<0.001
	Latency	0.005 ± 0.03	42	0.17	0.867
	Habitat	-4.856 ± 1.64	2	-2.96	0.098
	Latency × habitat	0.046 ± 0.04	42	1.20	0.238
Proportion of chicks fledged	Intercept	48.094 ± 513626.90	42	<0.01	>0.999
	Latency	-1.386 ± 16566.00	42	<0.01	>0.999
	Habitat	-46.752 ± 513626.90	2	<0.01	>0.999
	Latency × habitat	1.423 ± 16566.00	42	<0.01	>0.999
Fledgling body mass	Intercept	17.799 ± 1.02	40	17.46	<0.001
	Latency	0.005 ± 0.03	40	0.18	0.856
	Habitat	-3.359 ± 0.80	2	-4.19	0.053
	Hatching date[e]	0.108 ± 0.03	40	3.60	0.001
	Trapping status[f]	-1.426 ± 0.73	40	-1.95	0.058
	Latency × habitat	0.012 ± 0.04	40	0.33	0.746
Fledgling tarsus length	Intercept	20.404 ± 0.38	40	54.25	<0.001
	Latency	-0.007 ± 0.01	40	-0.75	0.460
	Habitat	-0.969 ± 0.33	2	-2.91	0.100
	Hatching date	0.023 ± 0.01	40	2.23	0.031
	Trapping status	-0.612 ± 0.25	40	-2.45	0.019
	Latency × habitat	0.008 ± 0.01	40	0.64	0.525

The table shows the results of mixed models (with study site as random factor; quasi-binomial error for hatching success and proportion of chicks fledged). The interaction term was re-inserted into the final models shown in Table S.III.5. The model estimates have high uncertainty for the proportion of chicks fledged due to lack of variance in the forest habitat.

[a] mean value of the dependent variable for the fastest pairs in forests

[b] effect of problem-solving latency (min) in forests

[c] effect of habitat (urban compared to forest) in the fastest pairs

[d] difference in the effect of problem-solving latency between urban and forest habitats

[e] number of days since 1st of May

[f] at least one vs. none of the parents trapped

Table S.III.6: Effects of neophobia, response to predation risk, and response to human disturbance on breeding success (n = 48 pairs with valid data in the food-acquisition test).

Dependent variable	Predictors	b ± SE	df	t	p
Clutch size	Neophobia[a]	-0.00 ± 0.00	35	-0.07	0.945
	Predation risk[b]	-0.64 ± 1.25	30	-0.51	0.614
	Human disturbance[c]	1.60 ± 1.87	31	0.85	0.401
Hatching success	Neophobia	0.00 ± 0.00	35	0.99	0.331
	Predation risk	-2.82 ± 2.16	30	-1.31	0.201
	Human disturbance	3.02 ± 3.26	31	0.93	0.362
Number of fledglings	Neophobia	0.00 ± 0.00	35	0.14	0.894
	Predation risk	-1.92 ± 1.58	30	-1.21	0.234
	Human disturbance	1.41 ± 2.73	31	0.52	0.609
Proportion of chicks fledged	Neophobia	-0.00 ± 0.00	36	-1.00	0.326
	Predation risk	0.73 ± 0.60	31	1.19	0.243
	Human disturbance	0.87 ± 1.30	32	0.65	0.520
Fledgling body mass	Neophobia	-0.00 ± 0.00	35	-0.34	0.738
	Predation risk	-0.91 ± 1.46	30	-0.62	0.538
	Human disturbance	0.83 ± 2.31	31	0.36	0.722
Fledgling tarsus length	Neophobia	0.00 ± 0.00	35	1.39	0.173
	Predation risk	0.09 ± 0.53	30	0.17	0.870
	Human disturbance	-1.44 ± 0.84	31	-1.72	0.095

The table shows the effects of each predictor separately inserted in the initial mixed models (with study site as random factor; quasi-binomial error for hatching success and proportion of chicks fledged) of the respective dependent variable (for full description of initial models, see Chapter 3.2.2.).

[a] latency to enter nestbox in neophobia test (mean values of the pair in seconds)

[b] difference in nest visit rate (visits after predator stimulus – visits after control; see methods in **Chapter III**)

[c] difference in nest visit rate (visits after human stimulus – visits before human stimulus; see methods in **Chapter III**)

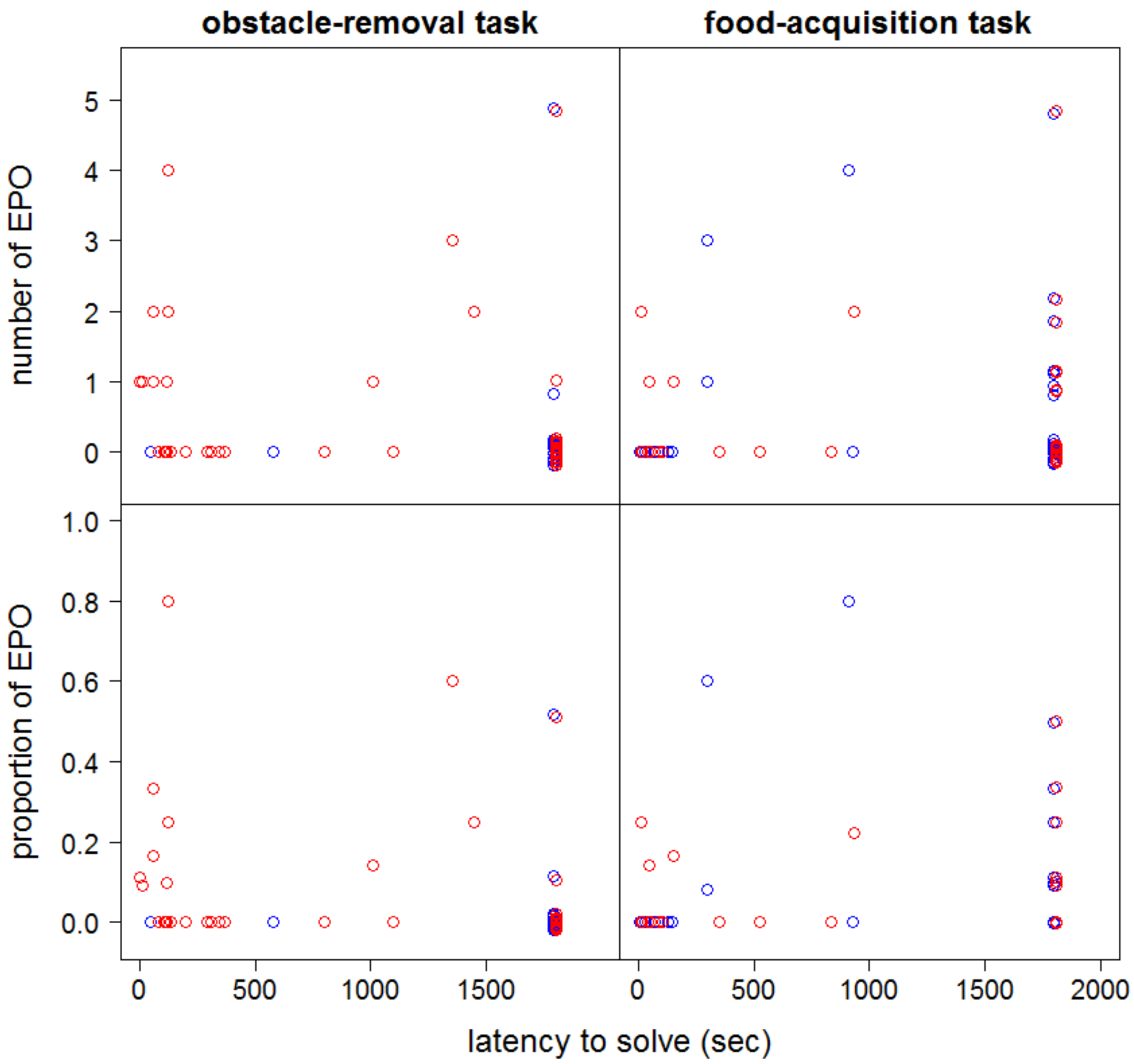

Figure S.IV.1: Relationships between the latency to solve each task by each sex (females: red symbols, males: blue symbols) and EPP expressed as the number or proportion of EPO in the social nest (for statistics, see Table S.IV.1).

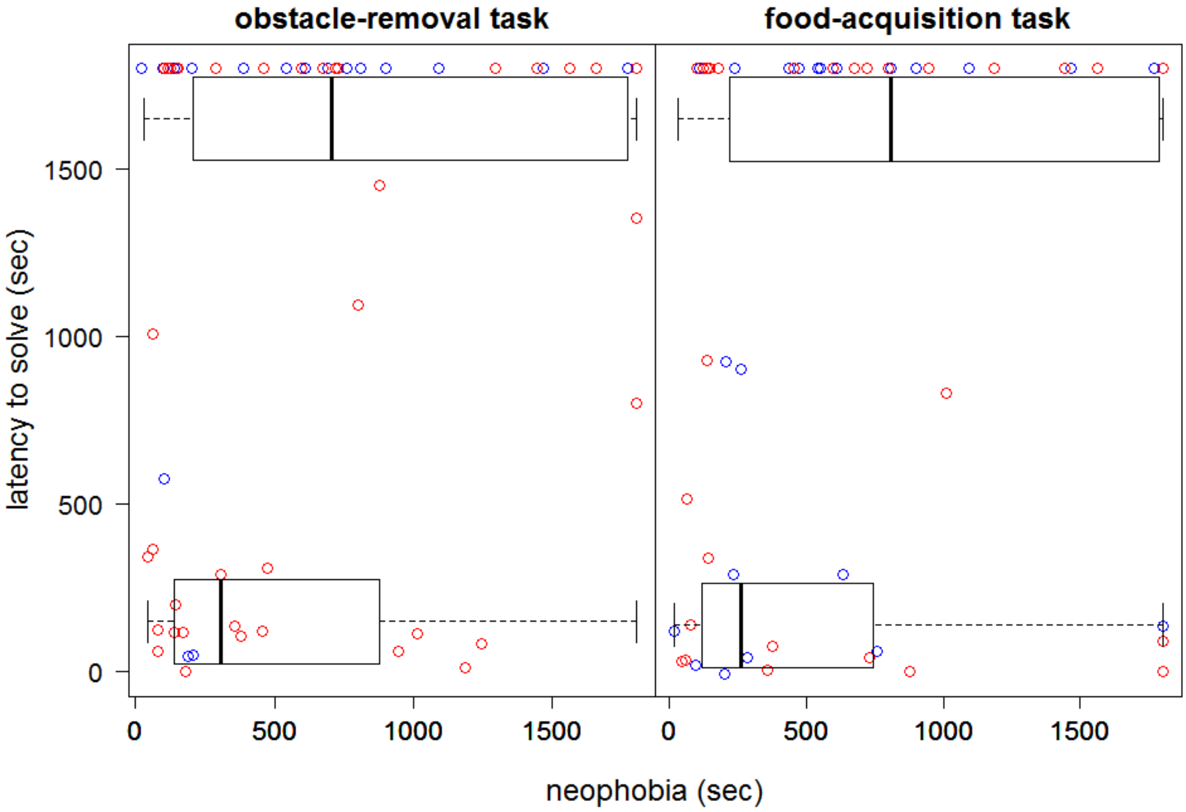

Figure S.IV.2. Problem-solving latencies in relation to neophobia (latency to enter nest box in the novel object test) in females (red symbols) and males (blue symbols). The two box plots in each panel represent the distribution (median, interquartile range, and total range) of neophobia (both sexes pooled) in solvers (lower box) and non-solvers (upper box). For statistics, see Table S.IV.5.

Table S.IV.1: Spearman rank-correlations between the latency to solve each task by each sex and EPP expressed as the number of EPO in the social nest; statistics in brackets refer to EPP expressed as the proportion of EPO among all offspring in the social nest.

Task	Sex	n	r_s	p
Obstacle-removal	Females	40	-0.36 (-0.36)	0.023 (0.021)
	Males	21	0.13 (0.13)	0.569 (0.569)
Food-acquisition	Females	31	0.08 (0.05)	0.677 (0.776)
	Males	28	0.13 (0.13)	0.500 (0.502)

Problem-solving latency of each parent was calculated as the time from the bird's first arrival to the platform on the nest box until it solved. Birds that did not solve were assigned the maximal latency (30 minutes). Birds whose mate had solved the task were omitted from the analysis of the respective task because their performance could not be quantified. For further details see Figure S.IV.1 and Preiszner et al. (2017).

Table S.IV.2: Relationships between EPP (presence or absence of EPO in the social nest) as explanatory variable and problem-solving latency in each task by each sex as dependent variable, including the individuals whose mate had solved the task as censored observations in Cox's proportional hazards models.

Task	Sex	n	e^b (95% CI)	z	p
Obstacle-removal	Females	43	3.123 (1.345; 7.254)	2.648	0.008
	Males	43	3.623×10^{-9} (0; ∞)	-0.001	0.999
Food-acquisition	Females	41	0.725 (0.223; 2.358)	-0.535	0.592
	Males	41	0.665 (0.172; 2.579)	-0.590	0.555

Instead of omitting the birds whose mate had solved the task, this analysis takes the information into account that these birds did not solve before their mate did (i.e. test time for these birds was shorter than 30 min, according to their mate's solving latency). Exponentially transformed parameter estimates (e^b) with 95% confidence intervals (CI) show the proportional change of hazard ratio (expressing the chance of solving the task) in response to the presence of EPO in the nest.

Table S.IV.3: Odds ratios of having extra-pair offspring in the brood, in relation to the sex of the solver parent in the obstacle-removal task (*n*= 43 pairs), using Firth's penalized-likelihood logistic regression.

Model parameters	*OR* (95% CI)	χ^2	*p*
Unsuccessful pairs	0.15 (0.03, 0.48)	11.54	<0.001
Pairs with solver female[a]	5.54 (1.30, 32.88)	5.46	0.019
Pairs with solver male[a]	0.94 (0.01, 15.71)	0.001	0.971

Odds ratios (*OR*) and their 95% confidence intervals (CI) were calculated from the parameter estimates of a logistic regression model with a bias-reduced maximum likelihood estimator (using package 'logistf'). This method circumvents the problem of separation, i.e. when there is no observed variance in the dependent variable in one or more groups defined by the predictor variable(s), leading to inaccurate odds-ratio estimates (as in Table IV.2 for solver males). Note that this method cannot accommodate random effects, however; so site is not included here.

[a] These estimates express the differences from the unsuccessful pairs.

Table S.IV.4: Odds ratios (*OR*) of having extra-pair offspring in the brood, in relation to first egg date, within-pair relatedness, and male age, calculated from linear mixed-effects models with quasi-binomial error distribution and site as random factor.

Model parameters	*OR* (95% CI)	df	*t*	*p*
a) Model with sex of solver parent and first egg date				
Unsuccessful pairs	0.34 (0.03, 3.52)	36	-0.93	0.357
Pairs with solver female	5.98 (1.03, 34.92)	36	2.10	0.043
Pairs with solver male	<0.01 (0, ∞)	36	<0.01	>0.999
First egg date	0.95 (0.78, 1.15)	36	-1.05	0.302
b) Model with sex of solver parent and within-pair relatedness				
Unsuccessful, unrelated pairs	0.11 (0.02, 0.51)	36	-2.71	0.010
Pairs with solver female	6.62 (1.13, 38.63)	36	2.10	0.043
Pairs with solver male	<0.01 (0, ∞)	36	<0.01	>0.999
Related pairs	1.79 (0.31, 10.43)	36	0.67	0.505
c) Model with sex of solver parent and male age				
Unsuccessful pairs, young males	0.21 (0.03, 1.49)	35	-1.54	0.132
Pairs with solver female	6.59 (1.13, 38.46)	35	2.11	0.042
Pairs with solver male	<0.01 (0, ∞)	35	<0.01	>0.999
Males of unknown age	0.71 (0.07, 7.44)	35	-0.29	0.775
Older males	0.46 (0.08, 2.67)	35	-0.87	0.392

Table S.IV.5: Cox's proportional hazards models of the latency to solve each task in relation to neophobia (latency to enter nest box in the novel object test).

Task	Sex	*n*	e^b (95% CI)	*z*	*p*
Obstacle-removal	Females	40	0.999 (0.998; 1.000)	-1.49	0.137
	Males	21	0.996 (0.989; 1.002)	-1.34	0.180
Food-acquisition	Females	31	0.999 (0.998; 1.001)	-0.94	0.348
	Males	28	0.998 (0.997; 1.000)	-1.69	0.091

Exponentially transformed parameter estimates (e^b) with 95% confidence intervals (CI) show the proportional change of hazard ratio (expressing the chance of solving the task) in response to a 1-sec increase in neophobia.

A/III Supplementary Material to Chapter VI

Below we provide a detailed account on the availability of each type of additional information and the distribution of data that we collected from the studies on the mortality of captive house sparrows. For the availability and distribution of mortality data, see Table VI.2 and Table VI.3.

Geography and range: Most of the studies were carried out in Europe (44.4%) and North America (45.0%); note that two of the latter studies included birds from Panama, Central America (Martin II 2005; Martin II and Fitzgerald 2005). Rest of the studies were from Asia (6.5%), Australia (2.8%) and Africa (0.9%) (Figure S.VI.1).

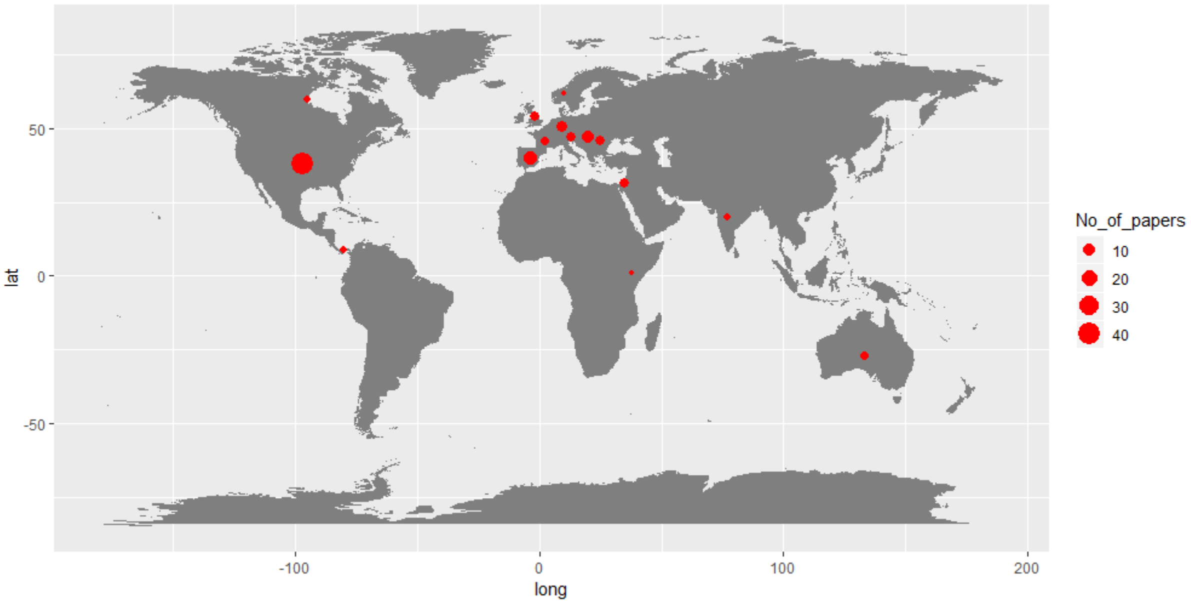

Figure S.VI.1: Geographic distribution of the reviewed studies.

Studies were equally represented within and outside the native range of house sparrows (50.0% each). Out of the 10 studies that involved planned death of the study subjects (e.g. testing avian pathogens or pesticide effects), 9 were carried out outside the native range of the species. However, availability of mortality data was higher in the studies originating from the native range of the species than from outside (57.4% and 37.0% respectively), and this difference was statistically significant (Pearson's Chi-squared test; $\chi^2_1 = 4.50$, $p = 0.034$). The larger proportion of mortality data reporting within the native range of house sparrows, along with the fact that studies that involved planned death of birds originated almost exclusively from outside of its native range, suggests a geographically different attitude towards the importance of house sparrow mortality. Latter difference in attitude is probably associated with the local perception of the species; in its introduced range it is considered a pest (Anderson 2006), whereas in parts of its native range its population suffers massive declines raising awareness and making it a protected species in some countries (Baillie et al. 2010).

Year of publication: The majority of relevant research is recent, since 51.5% of the reviewed 103 papers are from the past 10 years, whereas only 7.8% of them are dated between 1980 and 1989. This indicates an increasing trend of using captive house sparrows as model organisms.

Length of captivity: Due to the huge variability of the study types, and many times to the lack of clarity on the length of captivity, we often had to estimate it based on available information (e.g. when paper stated 2-4 weeks, we estimated 21 days). In 7.4% of the studies we were not able to determine the time spent in captivity at all. The length of captivity ranged between 1 and 1460 days (median = 79.0; mean ± SE = 155.7 ± 23.8 days). 7.4% of the studies involved maximum one week of captivity and 13.0% lasted for a year or longer.

Age: Almost half of the studies (44.4%) used only adult birds, while only 3 studies involved exclusively juveniles. 26.9% of the reviewed studies involved both age classes, and almost an equal amount (25.9%) revealed no data on the age of birds. Mortality data for juveniles were only available in two studies, preventing a formal comparison between age classes in captivity.

Sex: In 86.1% of the studies there was information available regarding the sex of the studied birds. Only 2 studies dealt with females only, whereas 24.1% involved exclusively males, and 60.2% of the reviewed studies used both sexes. In natural populations there is a difference in mortality rates between the two sexes (reviewed in Anderson 2006), but in the reviewed studies the lack of sufficient data for females made such comparisons impossible.

Sample size: Determining the number of birds used in the studies was sometimes challenging, as many times authors did not declare it explicitly, but it was available e.g. from figures and tables as treatment group sizes. In two studies sample size data were unavailable. In some cases, we used subsamples of the given study or we could only determine the minimum number of birds used. Number of birds used in the studies ranged between 6-192 individuals (median = 43.5; mean ± SE = 56.9 ± 4.51).

Housing: In most cases birds were kept exclusively indoors or outdoors; 43.5% and 31.5%, respectively. A smaller portion, 11.1% of the studies transferred birds between indoor and outdoor facilities at some point, and 6.5% used “semi-outdoor” aviaries (of the latter all but one used the same setup, see e.g. Laucht et al. 2010). There was no information available on this issue in 7.4% of the studies.

Group size: Data on group size (number of birds in the same cage or aviary) were available in 88.9% of the reviewed studies, ranging between 1-96 individuals per group. However, more than half of these studies only provided a range, or minimum, or maximum number of birds housed together. In the 47 studies where group size was clearly determinable, the median was 6 birds (mean ± SE = 13.0 ± 3.0).

Treatments: In 13.0% of the studies (27.5% of studies with data on mortality) we suspected that treatment could have affected mortality of birds. For example, infections could affect mortality, but testosterone (e.g. Schwabl et al. 2012) and corticosterone (e.g. Grace et al. 2017) are also known to do so, therefore such studies could bias mortality data.

Study scope: Though determining the scope of a study is sometimes ambiguous, we labelled 49.1% of the studies as behavioural and 45.4% as physiological topics. The rest (5.5%) is equally split between parasitological and methodological studies. Mortality data were equally available regardless of the scope of the study (46.9% in physiology, 49.1% in behaviour).

List of papers reviewed in ***Chapter VI***

Aharon-Rotman Y, Buchanan KL, Klaassen M, Buttemer WA (2017) An experimental examination of interindividual variation in feather corticosterone content in the house sparrow, *Passer domesticus* in southeast Australia. Gen Comp Endocrinol 244:93–100. doi: 10.1016/j.ygcen.2015.12.010

Ahmad S, Saleem Z, Jabeen F, et al (2018) Potential of natural repellents methylanthranilate and anthraquinone applied on maize seeds and seedlings against house sparrow (*Passer domesticus*) in captivity. Brazilian J Biol 78:667–672. doi: 10.1590/1519-6984.171686

Alonso JC (1984) Kreuzung spanischer Haus- (*Passer domesticus*) und Weidensperlinge (*Passer hispaniolensis*) in Gefangenschaft. J Ornithol 125:339–340. doi: 10.1007/BF01640484

Balcomb R, Bowen CA, Wright D, Law M (1984) Effects on wildlife of at-planting corn applications of granular carbofuran. J Wildl Manage 48:1353–1359. doi: 10.2307/3801796

Barnard CJJ, Sibly RMM (1981) Producers and scroungers: A general model and its application to captive flocks of house sparrows. Anim Behav 29:543–550. doi: 10.1016/S0003-3472(81)80117-0

Beal KG (1978) Temperature-dependent reduction of individual distance in captive house-sparrows. Auk 95:195–196. doi: 10.2307/4085517

Belmaker A, Motro U, Feldman MW, Lotem A (2012) Learning to choose among social foraging strategies in adult house sparrows (*Passer domesticus*). Ethology 118:1111–1121. doi: 10.1111/eth.12013

Best LB, Gionfriddo JP (1994a) Effects of surface texture and shape on grit selection by house sparrows and northern bobwhite. Wilson Bull 106:689–695

Best LB, Gionfriddo JP (1994b) House sparrow preferential consumption of carriers used for pesticide granules. Environ Toxicol Chem 13:919–925. doi: 10.1002/etc.5620130610

Bhardwaj SK, Anushi (2006) Effect of photoperiod length on body mass and testicular growth in the house sparrow (*Passer domesticus*) and brahminy myna (Sturnus pagodarum). Reprod Nutr Dev 46:69–76. doi: 10.1051/rnd

Bókony V, Kulcsár A, Liker A (2010) Does urbanization select for weak competitors in house sparrows? Oikos 119:437–444. doi: 10.1111/j.1600-0706.2009.17848.x

Bókony V, Lendvai ÁZ, Liker A, et al (2006) Multiple cues in status signalling: the role of wingbars in aggressive interactions of male house sparrows. Ethology 112:947–954. doi: 10.1111/j.1439-0310.2006.01246.x

Bonneaud C, Mazuc J, Gonzalez G, et al (2003) Assessing the cost of mounting an immune response. Am Nat 161:367–379. doi: 10.1086/346134

Broggi J, García O, Miranda F, et al (2013) Immune response to Newcastle disease virus vaccination in a wild passerine. J Wildl Dis 49:1004–1008. doi: 10.7589/2012-10-266

Buttemer WA, Warne S, Bech C, Astheimer LB (2008) Testosterone effects on avian basal metabolic rate and aerobic performance: Facts and artefacts. Comp Biochem Physiol - A Mol Integr Physiol 150:204–210. doi: 10.1016/j.cbpa.2006.06.047

Caviedes-Vidal E, Karasov WH (2001) Developmental changes in digestive physiology of nestling house sparrows, *Passer domesticus*. Physiol Biochem Zool 74:769–782. doi: 10.1086/322966

Cohen AA, Hau M, Wikelski M (2008) Stress, metabolism, and antioxidants in two wild passerine bird species. Physiol Biochem Zool 81:463–472. doi: 10.1086/589548

Coon CAC, Garcia-Longoria L, Martin LB, et al (2016) Malaria infection negatively affects feather growth rate in the house sparrow *Passer domesticus*. J Avian Biol 47:779–787. doi: 10.1111/jav.00942

Cramer ERA, Laskemoen T, Stensrud E, et al (2015) Morphology-function relationships and repeatability in the sperm of Passer sparrows. J Morphol 276:. doi: 10.1002/jmor.20346

Cushing TLL, Schat KAA, States SLL, et al (2011) Characterization of the host response in systemic isosporosis (atoxoplasmosis) in a colony of captive american goldfinches (*Spinus tristis*) and house sparrows (P*asser domesticus*). Vet Pathol 48:985–992. doi: 10.1177/0300985810391114

de Hierro MDGL, De Neve L (2010) Pigment limitation and female reproductive characteristics influence egg shell spottiness and ground colour variation in the house sparrow (*Passer domesticus*). J Ornithol 151:833–840. doi: 10.1007/s10336-010-0520-1

De Neve L, Ibañez-Alamo JD, Soler M (2010) Age-and sex-related morphological and physiological differences influence escape capacity in House Sparrows (*Passer domesticus*). Can J Zool 88:1021–1031. doi: 10.1139/Z10-067

Dor R, Lotem A (2009) Heritability of nestling begging intensity in the house sparrow (*Passer domesticus*). Evolution (N Y) 63:738–748. doi: 10.1111/j.1558-5646.2008.00598.x

Elliott JE, Hindmarch S, Albert CA, et al (2014) Exposure pathways of anticoagulant rodenticides to nontarget wildlife. Environ Monit Assess 186:865–906. doi: 10.1007/s10661-013-3422-x

Fischer CP, Wright-Lichter J, Romero LM (2018) Chronic stress and the introduction to captivity: How wild house sparrows (*Passer domesticus*) adjust to laboratory conditions. Gen Comp Endocrinol 259:85–92. doi: 10.1016/j.ygcen.2017.11.007

Fitzgerald JA (1990) Effects of long and short photoperiods on nutrient preferences of migratory dark-eyed juncos and non-migratory house sparrows. Bird Behav 8:87–94. doi: 10.3727/015613890791784254

Gao S, Sanchez C, Deviche PJ (2017) Corticosterone rapidly suppresses innate immune activity in the house sparrow (*Passer domesticus*). J Exp Biol 220:322–327. doi: 10.1242/jeb.144378

Gill H, Paperna I (2008) Proliferative visceral Isospora (atoxoplasmosis) with morbid impact on the Israeli sparrow *Passer domesticus biblicus* Hartert, 1904. Parasitol Res 103:493–499. doi: 10.1007/s00436-008-0986-4

Gill H, Paperna I (2005) Leucocytozoonosis in the Israeli sparrow, *Passer domesticus biblicus* Hartert 1904. Parasitol Res 96:373–377. doi: 10.1007/s00436-005-1352-4

Gionfriddo JP, Best LB (1996) Grit color selection by house sparrows and northern bobwhites. J Wildl Manage 60:836–842. doi: 10.2307/3802384

Girndt A, Chng CWT, Burke T, Schroeder J (2018) Male age is associated with extra-pair paternity, but not with extra-pair mating behaviour. Sci Rep 8:1–10. doi: 10.1038/s41598-018-26649-1

Girndt A, Cockburn G, Sánchez-Tójar A, et al (2017) Method matters: Experimental evidence for shorter avian sperm in faecal compared to abdominal massage samples. PLoS One 12:1–17. doi: 10.1371/journal.pone.0182853

Goldstein DL, Zahedi A (1990) Variation in osmoregulatory parameters of captive and wild house sparrows (*Passer domesticus*). Auk 107:533–538. doi: 10.1093/auk/107.3.533

Gonzalez G, Anders GS, Møller AP, et al (1999) Immunocompetence and condition-dependent sexual advertisement in male house sparrows (*Passer domesticus*). J Anim Ecol 68:1225–1234. doi: 10.1046/j.1365-2656.1999.00364.x

Gonzalez G, Sorci G, Smith LC, de Lope F (2002) Social control and physiological cost of cheating in status signalling male house sparrows (*Passer domesticus*). Ethology 108:289–302. doi: 10.1046/j.1439-0310.2002.00779.x

Gormally BMG, Fuller R, McVey M, Romero LM (2019) DNA damage as an indicator of chronic stress: Correlations with corticosterone and uric acid. Comp Biochem Physiol -Part A Mol Integr Physiol 227:116–122. doi: 10.1016/j.cbpa.2018.10.007

Gormally BMG, Romero LM (2018) House sparrows (*Passer domesticus*) adjusted hypothalamic-pituitary-adrenal axis negative feedback and perch hopping activities in response to a single repeated stimulus. J Exp Zool Part A Ecol Integr Physiol 329:597–605. doi: 10.1002/jez.2229

Gormally BMG, Wright-Lichter J, Reed JM, Romero LM (2018) Physiological and behavioral responses of house sparrows to repeated stressors. PeerJ 6:e4961. doi: 10.7717/peerj.4961

Grace JK, Froud L, Meillère A, Angelier F (2017) House sparrows mitigate growth effects of post-natal glucocorticoid exposure at the expense of longevity. Gen Comp Endocrinol 253:1–12. doi: 10.1016/j.ygcen.2017.08.011

Greenman CG, Martin II LB, Hau M (2005) Reproductive state, but not testosterone, reduces immune function in male house sparrows (*Passer domesticus*). Physiol Biochem Zool 78:60–68. doi: 10.1086/425194

Greig-Smith PW (1987) Aversions of starlings and sparrows to unfamiliar, unexpected or unusual flavours and colours in food. Ethology 74:155–163. doi: 10.1111/j.1439-0310.1987.tb00928.x

Greig-Smith PW, Rowney CM (1987) Effects of colour on the aversions of starlings and house sparrows to five chemical repellents. Crop Prot 6:402–409. doi: 10.1016/0261-2194(87)90075-5

Hau M, Dominguez OA, Evrard HC (2004) Testosterone reduces responsiveness to nociceptive stimuli in a wild bird. Horm Behav 46:165–170. doi: 10.1016/j.yhbeh.2004.02.007

Hau M, Gwinner E (1992) Circadian entrainment by feeding cycles in house sparrows, *Passer domesticus*. J Comp Physiol A 170:403–409. doi: 10.1007/BF00191457

Hegner RE, Wingfield JC (1987) Social Status and Circulating Levels of Hormones in Flocks of House Sparrows, *Passer domesticus*. Ethology 76:1–14. doi: 10.1111/j.1439-0310.1987.tb00667.x

Hoshooley JS, Sherry DF (2007) Greater hippocampal neuronal recruitment in food-storing than in non-food-storing birds. Dev Neurobiol 67:406–414. doi: 10.1002/dneu.22087

Huber N, Fusani L, Ferretti A, et al (2017) Measuring short-term stress in birds: Comparing different endpoints of the endocrine-immune interface. Physiol Behav 182:46–53. doi: 10.1016/j.physbeh.2017.09.017

Kimball RT (1996) Female choice for male morphological traits in house sparrows, *Passer domesticus*. Ethology 102:639–648. doi: 10.1111/j.1439-0310.1996.tb01155.x

Kuhlman JR, Martin LB (2010) Captivity affects immune redistribution to skin in a wild bird. Funct Ecol 24:830–837. doi: 10.1111/j.1365-2435.2010.01710.x

Lattin CR, Bauer CM, de Bruijn R, Romero LM (2012) Hypothalamus-pituitary-adrenal axis activity and the subsequent response to chronic stress differ depending upon life history stage. Gen Comp Endocrinol 178:494–501. doi: 10.1016/j.ygcen.2012.07.013

Lattin CR, Pechenenko A V., Carson RE (2017) Experimentally reducing corticosterone mitigates rapid captivity effects on behavior, but not body composition, in a wild bird. Horm Behav 89:121–129. doi: 10.1016/j.yhbeh.2016.12.016

Lattin CR, Romero LM (2014) Chronic stress alters concentrations of corticosterone receptors in a tissue-specific manner in wild house sparrows (*Passer domesticus*). J Exp Biol 217:2601–2608. doi: 10.1242/jeb.103788

Laucht S, Dale J (2012a) Development of badges of status in captive male house sparrows (*Passer domesticus*) in relation to the relative ornamentation of flock-mates. Ethology 118:644–653. doi: 10.1111/j.1439-0310.2012.02053.x

Laucht S, Dale J (2012b) Correlations of condition, testosterone, and age with multiple ornaments in male house sparrows: patterns and implications. Condor 114:865–873. doi: 10.1525/cond.2012.110194

Laucht S, Dale J, Mutzel A, Kempenaers B (2011) Individual variation in plasma testosterone levels and its relation to badge size in House Sparrows *Passer domesticus*: It's a night-and-day difference. Gen Comp Endocrinol 170:501–508. doi: 10.1016/j.ygcen.2010.11.007

Laucht S, Kempenaers B, Dale J (2010) Bill color, not badge size, indicates testosterone-related information in house sparrows. Behav Ecol Sociobiol 64:1461–1471. doi: 10.1007/s00265-010-0961-9

Lee KA, Martin II LB, Wikelski MC (2005) Responding to inflammatory challenges is less costly for a successful avian invader, the house sparrow (*Passer domesticus*), than its less-invasive congener. Oecologia 145:244–251. doi: 10.1007/s00442-005-0113-5

Lendvai ÁZ, Barta Z, Liker A, Bókony V (2004) The effect of energy reserves on social foraging: hungry sparrows scrounge more. Proc R Soc B Biol Sci 271:2467–2472. doi: 10.1098/rspb.2004.2887

Lendvai ÁZ, Chastel O (2008) Experimental mate-removal increases the stress response of female house sparrows: The effects of offspring value? Horm Behav 53:395–401. doi: 10.1016/j.yhbeh.2007.11.011

Lendvai ÁZ, Ouyang JQ, Schoenle LA, et al (2014) Experimental food restriction reveals individual differences in corticosterone reaction norms with no oxidative costs. PLoS One 9:Article number e110564. doi: 10.1371/journal.pone.0110564

Liker A, Barta Z (2002) The effects of dominance on social foraging tactic use in house sparrows. Behaviour 139:1061–1076. doi: 10.1163/15685390260337903

Liker A, Barta Z (2001) Male badge size predicts dominance against females in House Sparrows. Condor 103:151–157. doi: 10.1650/0010-5422(2001)103[0151:MBSPDA]2.0.CO;2

Liker A, Bókony V (2009) Larger groups are more successful in innovative problem solving in house sparrows. Proc Natl Acad Sci U S A 106:7893–7898. doi: 10.1073/pnas.0900042106

Liker A, Papp Z, Bókony V, Lendvai ÁZ (2008) Lean birds in the city: body size and condition of house sparrows along the urbanization gradient. J Anim Ecol 77:789–95. doi: 10.1111/j.1365-2656.2008.01402.x

Love AC, Lovern MB, DuRant SE (2017) Captivity influences immune responses, stress endocrinology, and organ size in house sparrows (*Passer domesticus*). Gen Comp Endocrinol 252:18–26. doi: 10.1016/j.ygcen.2017.07.014

Lukasch B, Westerdahl H, Strandh M, et al (2017) Genes of the major histocompatibility complex highlight interactions of the innate and adaptive immune system. PeerJ 5:e3679. doi: 10.7717/peerj.3679

Martin II LB (2005) Trade-offs between molt and immune activity in two populations of house sparrows (*Passer domesticus*). Can J Zool 83:780–787. doi: 10.1139/Z05-062

Martin II LB, Fitzgerald L (2005) A taste for novelty in invading house sparrows, *Passer domesticus*. Behav Ecol 16:702–707. doi: 10.1093/beheco/ari044

Martin II LB, Han P, Kwong J, Hau M (2006) Cutaneous immune activity varies with physiological state in female house sparrows (*Passer domesticus*). Physiol Biochem Zool 79:775–783. doi: 10.1086/504608

Martin LB, Brace AJ, Urban A, et al (2012) Does immune suppression during stress occur to promote physical performance? J Exp Biol 215:4097–4103. doi: 10.1242/jeb.073049

Martin LB, Kidd L, Liebl AL, Coon CAC (2011) Captivity induces hyper-inflammation in the house sparrow (*Passer domesticus*). J Exp Biol 214:2579–2585. doi: 10.1242/jeb.057216

Martin LB, Liebl AL (2014) Physiological flexibility in an avian range expansion. Gen Comp Endocrinol 206:227–234. doi: 10.1016/j.ygcen.2014.07.016

McGraw KJ, Dale J, Mackillop EA (2003) Social environment during molt and the expression of melanin-based plumage pigmentation in male house sparrows (*Passer domesticus*). Behav Ecol Sociobiol 53:116–122. doi: 10.1007/s00265-002-0558-z

Moreno-Rueda G (2010) Uropygial gland size correlates with feather holes, body condition and wingbar size in the house sparrow *Passer domesticus*. J Avian Biol 41:229–236. doi: 10.1111/j.1600-048X.2009.04859.x

Moreno-Rueda G, Soler M (2002) Cría En Cautividad Del Gorrión Común *Passer Domesticus*. Ardeola 49:11–17

Mutzel A, Kempenaers B, Laucht S, et al (2011) Circulating testosterone levels do not affect exploration in house sparrows: Observational and experimental tests. Anim Behav 81:731–739. doi: 10.1016/j.anbehav.2011.01.001

Needham KB, Kucera AC, Heidinger BJ, Greives TJ (2017) Repeated immune challenges affect testosterone but not sperm quality. J Exp Zool Part A Ecol Integr Physiol 327:398–406. doi: 10.1002/jez.2110

Nemeth NM, Thomas NO, Orahood DS, et al (2010) Shedding and serologic responses following primary and secondary inoculation of house sparrows (*Passer domesticus*) and European starlings (*Sturnus vulgaris*) with low-pathogenicity avian influenza virus. Avian Pathol 39:411–418. doi: 10.1080/03079457.2010.513043

Pap PL, Czirják GÁ, Vágási CI, et al (2010) Sexual dimorphism in immune function changes during the annual cycle in house sparrows. Naturwissenschaften 97:891–901. doi: 10.1007/s00114-010-0706-7

Pap PL, Sesarman A, Vágási CI, et al (2014) No evidence for parasitism-linked changes in immune function or oxidative physiology over the annual cycle of an avian species. Physiol Biochem Zool 87:729–739. doi: 10.1086/676934

Pap PL, Vágási CI, Czirják GA, et al (2011) The Effect of Coccidians on the Condition and Immune Profile of Molting House Sparrows (*Passer Domesticus*). Auk 128:330–339. doi: 10.1525/auk.2011.10142

Pap PL, Vágási CI, Czirják GÁ, Barta Z (2008) Diet quality affects postnuptial molting and feather quality of the house sparrow (*Passer domesticus*): interaction with humoral immune function? Can J Zool 86:834–842. doi: 10.1139/Z08-060

Parrish JW, Mote ML (1984) Serum chemical levels in captive female House Sparrows. Wilson Bull 96:138–141

Poiani A, Goldsmith AR, Evans MR (2000) Ectoparasites of house sparrows (*Passer domesticus*): An experimental test of the immunocompetence handicap hypothesis and a new model. Behav Ecol Sociobiol 47:230–242. doi: 10.1007/s002650050660

Puerta M, Nava MP, Venero C, Veiga JP (1995) Hematology and plasma chemistry of house sparrows (*Passer domesticus*) along the summer months and after testosterone treatment. Comp Biochem Physiol -- Part A Physiol 110:303–307. doi: 10.1016/0300-9629(94)00187-X

Quay WB (1987) Spontaneous continuous release of spermatozoa and its predawn surge in male passerine birds. Gamete Res 16:83–92. doi: 10.1002/mrd.1120160110

Rich EL, Romero LM (2001) Daily and photoperiod variations of basal and stress-induced corticosterone concentrations in house sparrows (*Passer domesticus*). J Comp Physiol - B Biochem Syst Environ Physiol 171:543–547. doi: 10.1007/s003600100204

Romero LM, Reed JM (2008) Repeatability of baseline corticosterone concentrations. Gen Comp Endocrinol 156:27–33. doi: 10.1016/j.ygcen.2007.10.001

Roth II TC, Stocker K, Mauck R (2017) Morphological changes in hippocampal cytoarchitecture as a function of spatial treatment in birds. Dev Neurobiol 77:93–101. doi: 10.1002/dneu.22413

Salleh Hudin N, Strubbe D, Teyssier A, et al (2016) Predictable food supplies induce plastic shifts in avian scaled body mass. Behav Ecol 27:1833–1840. doi: 10.1093/beheco/arw108

Schwabl H, Holmes D, Strasser R, Scheuerlein A (2012) Embryonic exposure to maternal testosterone influences age-specific mortality patterns in a captive passerine bird. Age (Omaha) 34:87–94. doi: 10.1007/s11357-011-9222-8

Seress G, Bókony V, Heszberger J, Liker A (2011) Response to Predation Risk in Urban and Rural House Sparrows. Ethology 117:896–907. doi: 10.1111/j.1439-0310.2011.01944.x

Seress G, Bókony V, Pipoly I, et al (2012) Urbanization, nestling growth and reproductive success in a moderately declining house sparrow population. J Avian Biol 43:403–414. doi: 10.1111/j.1600-048X.2012.05527.x

Soler M, Ruiz-Castellano C, del Carmen Fernández-Pinos M, et al (2011) House sparrows selectively eject parasitic conspecific eggs and incur very low rejection costs. Behav Ecol Sociobiol 65:1997–2005. doi: 10.1007/s00265-011-1209-z

Stafford TR, Best LB (1998) Effects of application rate on avian risk from granular pesticides. Environ Toxicol Chem 17:526–529. doi: 10.1897/1551-5028(1998)017<0526:EOAROA>2.3.CO;2

Stafford TR, Best LB (1997) Effects of granular pesticide formulations and soil moisture on avian exposure. Environ Toxicol Chem 16:1687–1693. doi: 10.1897/1551-5028(1997)016<1687:EOGPFA>2.3.CO;2

Stafford TR, Best LB, Fischer DL (1996) Effects of different formulations of granular pesticides on birds. Environ Toxicol Chem 15:1606–1611. doi: 10.1002/etc.5620150926

Tóth Z, Baldan D, Hoi H, Griggio M (2014) Food reduction has a limited effect on following relations in house sparrow flocks. Anim Behav 90:91–100. doi: 10.1016/j.anbehav.2014.01.018

Tóth Z, Bókony V, Lendvai ÁZ, et al (2009) Whom do the sparrows follow? The effect of kinship on social preference in house sparrow flocks. Behav Processes 82:173–177. doi: 10.1016/j.beproc.2009.06.003

Tóth Z, Tuliozi B, Baldan D, et al (2017) The effect of social connections on the discovery of multiple hidden food patches in a bird species. Sci Rep 7:1–9. doi: 10.1038/s41598-017-00929-8

Trivedi AK, Rani S, Kumar V (2006) Control of annual reproductive cycle in the subtropical house sparrow (*Passer domesticus*): evidence for conservation of photoperiodic control mechanisms in birds. Front Zool 3:Article number 12. doi: 10.1186/1742-9994-3-12

Vágási CI, Pătraș L, Pap PL, et al (2018) Experimental increase in baseline corticosterone level reduces oxidative damage and enhances innate immune response. PLoS One 13:e0192701. doi: 10.1371/journal.pone.0192701

Wikelski M, Martin LB, Scheuerlein A, et al (2008) Avian circannual clocks: Adaptive significance and possible involvement of energy turnover in their proximate control. Philos Trans R Soc B Biol Sci 363:411–423. doi: 10.1098/rstb.2007.2147

REFERENCES

Akçay E, Roughgarden J (2007) Extra-pair paternity in birds: review of the genetic benefits. Evol Ecol Res 9:855–868

Altshuler DL, Nunn AM (2001) Observational Learning in Hummingbirds. Auk 118:795–799

Anderson TR (2006) Biology of the ubiquitous house sparrow: from genes to populations. Oxford University Press Inc., Oxford, New York, U.S.A.

Aplin LM, Farine DR, Cockburn A, Thornton A (2015) Experimentally induced innovations lead to persistent culture via conformity in wild birds. Nature 518:538–541. doi: 10.1038/nature13998

Aplin LM, Farine DR, Morand-Ferron J, Sheldon BC (2012) Social networks predict patch discovery in a wild population of songbirds. Proc R Soc B Biol Sci 279:4199–4205. doi: 10.1098/rspb.2012.1591

Arct A, Drobniak SM, Cichoń M (2015) Genetic similarity between mates predicts extrapair paternity – a meta-analysis of bird studies. Behav Ecol 26:959–968. doi: 10.1093/beheco/arv004

Ashton BJ, Thornton A, Ridley AR (2019) Larger group sizes facilitate the emergence and spread of innovations in a group-living bird. Anim Behav 158:1–7. doi: 10.1016/j.anbehav.2019.10.004

Audet J-N, Ducatez S, Lefebvre L (2016) The town bird and the country bird: problem solving and immunocompetence vary with urbanization. Behav Ecol 27:637–644. doi: 10.1093/beheco/arv201

Audet J-N, Kayello L, Ducatez S, et al (2018) Divergence in problem-solving skills is associated with differential expression of glutamate receptors in wild finches. Sci Adv 4:eaao6369

Audet J-N, Lefebvre L (2017) What’s flexible in behavioral flexibility? Behav Ecol 28:943–947. doi: 10.1093/beheco/arx007

Baillie SR, Marchant JH, Leech DI, et al (2010) Breeding birds in the wider countryside: their conservation status 2010. – BTO Research Report no. 565. Thetford.

Bailly J, Scheifler R, Berthe S, et al (2015) From eggs to fledging: negative impact of urban habitat on reproduction in two tit species. J Ornithol. doi: 10.1007/s10336-015-1293-3

Belmaker A, Motro U, Feldman MW, Lotem A (2012) Learning to choose among social foraging strategies in adult house sparrows (Passer domesticus). Ethology 118:1111–1121. doi: 10.1111/eth.12013

Benson-Amram S, Holekamp KE (2012) Innovative problem solving by wild spotted hyenas. Proc R Soc B Biol Sci 279:4087–4095. doi: 10.1098/rspb.2012.1450

Bird CD, Emery NJ (2009) Insightful problem solving and creative tool modification by captive nontool-using rooks. Proc Natl Acad Sci U S A 106:10370–10375. doi: 10.1073/pnas.0901008106

Blakey JK (1994) Genetic evidence for extra-pair fertilizations in a monogamous passerine, the Great Tit *Parus major*. Ibis (Lond 1859) 136:457–462

Bókony V, Kulcsár A, Liker A (2010) Does urbanization select for weak competitors in house sparrows? Oikos 119:437–444. doi: 10.1111/j.1600-0706.2009.17848.x

Bókony V, Kulcsár A, Tóth Z, Liker A (2012a) Personality traits and behavioral syndromes in differently urbanized populations of House Sparrows (*Passer domesticus*). PLoS One 7:e36639. doi: 10.1371/journal.pone.0036639

Bókony V, Lendvai ÁZ, Liker A, et al (2006) Multiple cues in status signalling: the role of wingbars in aggressive interactions of male house sparrows. Ethology 112:947–954. doi: 10.1111/j.1439-0310.2006.01246.x

Bókony V, Lendvai ÁZ, Vágási CI, et al (2014) Necessity or capacity? Physiological state predicts problem-solving performance in house sparrows. Behav Ecol 25:124–135. doi: 10.1093/beheco/art094

Bókony V, Seress G, Nagy S, et al (2012b) Multiple indices of body condition reveal no negative effect of urbanization in adult house sparrows. Landsc Urban Plan 104:75–84. doi: 10.1016/j.landurbplan.2011.10.006

Boogert NJ, Fawcett TW, Lefebvre L (2011) Mate choice for cognitive traits: a review of the evidence in nonhuman vertebrates. Behav Ecol 22:447–459. doi: 10.1093/beheco/arq173

Boogert NJ, Monceau K, Lefebvre L (2010) A field test of behavioural flexibility in Zenaida doves (*Zenaida aurita*). Behav Processes 85:135–141. doi: 10.1016/j.beproc.2010.06.020

Boogert NJ, Reader SM, Hoppitt W, Laland KN (2008) The origin and spread of innovations in starlings. Anim Behav 75:1509–1518. doi: 10.1016/j.anbehav.2007.09.033

Boogert NJ, Reader SM, Laland KN (2006) The relation between social rank, neophobia and individual learning in starlings. Anim Behav 72:1229–1239. doi: 10.1016/j.anbehav.2006.02.021

Bostic DL, Banks RC (1966) A record of stingray predation by the brown pelican. Condor 68:515–516

Bouchard J, Goodyer W, Lefebvre L (2007) Social learning and innovation are positively correlated in pigeons (*Columba livia*). Anim Cogn 10:259–266. doi: 10.1007/s10071-006-0064-1

Brown WD, Smith AT, Moskalik B, Gabriel J (2006) Aggressive contests in house crickets: size, motivation and the information content of aggressive songs. Anim Behav 72:225–233. doi: 10.1016/j.anbehav.2006.01.012

Burfield I, van Bommel F (eds) (2004) Birds in Europe: population estimates, trends and conservation status. BirdLife International, Cambridge

Byrne RW (2003) Novelty in Deceit. In: Reader SM, Laland KN (eds) Animal innovation. Oxford University Press Inc., Oxford, United Kingdom, pp 237–260

Callander S, Bolton J, Jennions MD, Backwell PRY (2012) A farewell to arms: males with regenerated claws fight harder over resources. Anim Behav 84:619–622. doi: 10.1016/j.anbehav.2012.06.017

Carere C, Welink D, Drent PJ, et al (2001) Effect of social defeat in a territorial bird (*Parus major*) selected for different coping styles. Physiol Behav 73:427–433

Cauchard L, Angers B, Boogert NJ, et al (2017) An experimental test of a causal link between problem-solving performance and reproductive success in wild great tits. Front Ecol Evol 5:107. doi: 10.3389/fevo.2017.00107

Cauchard L, Boogert NJ, Lefebvre L, et al (2013) Problem-solving performance is correlated with reproductive success in a wild bird population. Anim Behav 85:19–26. doi: 10.1016/j.anbehav.2012.10.005

Chamberlain DE, Cannon AR, Toms MP, et al (2009) Avian productivity in urban landscapes: a review and meta-analysis. Ibis (Lond 1859) 151:1–18. doi: 10.1111/j.1474-919X.2008.00899.x

Charmantier A, Blondel J, Perret P, Lambrechts MM (2004) Do extra-pair paternities provide genetic benefits for female blue tits *Parus caeruleus*? J Avian Biol 35:524–532

Chow PKY, Lea SEG, Leaver LA (2016) How practice makes perfect: the role of persistence, flexibility and learning in problem-solving efficiency. Anim Behav 112:273–283. doi: 10.1016/j.anbehav.2015.11.014

Clavero M, García-Berthou E (2005) Invasive species are a leading cause of animal extinctions. Trends Ecol Evol 20:5451. doi: 10.1016/j.tree.2005.01.003

Cole EF, Morand-Ferron J, Hinks AE, Quinn JL (2012) Cognitive ability influences reproductive life history variation in the wild. Curr Biol 22:1808–1812. doi: 10.1016/j.cub.2012.07.051

Cole EF, Quinn JL (2012) Personality and problem-solving performance explain competitive ability in the wild. Proc R Soc B Biol Sci 279:1168–1175. doi: 10.1098/rspb.2011.1539

Cook MO, Weaver MJ, Hutton P, McGraw KJ (2017) The effects of urbanization and human disturbance on problem solving in juvenile house finches (*Haemorhous mexicanus*). Behav Ecol Sociobiol 71:85. doi: 10.1007/s00265-017-2304-6

Darimont CT, Fox CH, Bryan HM, Reimchen TE (2015) The unique ecology of human predators. Science (80-) 349:858–861

de Kort SR, Emery NJ, Clayton NS (2006) Food sharing in jackdaws, Corvus monedula: What, why and with whom? Anim Behav 72:297–304. doi: 10.1016/j.anbehav.2005.10.016

de Satgé J, Strubbe D, Elst J, et al (2019) Urbanisation lowers great tit (*Parus major*) breeding success at multiple spatial scales. J Avian Biol. doi: 10.1111/jav.02108

Deary IJ, Johnson W, Houlihan LM (2009) Genetic foundations of human intelligence. Hum Genet 126:215–232. doi: 10.1007/s00439-009-0655-4

Derksen S, Keselmanf J, Keselman HJ (1992) Backward, forward and stepwise automated subset selection algorithms: frequency of obtaining authentic and noise variables. Br J Math Stat Psychol 45:265–282

Dingemanse NJ, Both C, Drent PJ, et al (2002) Repeatability and heritability of exploratory behaviour in great tits from the wild. Anim Behav 64:929–938. doi: 10.1006/anbe.2002.2006

Diquelou MC, Griffin AS, Sol D (2015) The role of motor diversity in foraging innovations: a cross-species comparison in urban birds. Behav Ecol 27:584–591. doi: 10.1093/beheco/arv190

Drea CM, Wallen K (1999) Low-status monkeys “play dumb” when learning in mixed social groups. Proc Natl Acad Sci U S A 96:12965–12969

Ducatez S, Audet J-N, Rodriguez JR, et al (2017) Innovativeness and the effects of urbanization on risk-taking behaviors in wild Barbados birds. Anim Cogn 20:33–42. doi: 10.1007/s10071-016-1007-0

Elias DO, Hebets EA, Hoy RR (2006) Female preference for complex/novel signals in a spider. Behav Ecol 17:765–771. doi: 10.1093/beheco/arl005

Emery NJ (2006) Cognitive ornithology: the evolution of avian intelligence. Philos Trans R Soc B Biol Sci 361:23–43. doi: 10.1098/rstb.2005.1736

Etienne AS (1984) The meaning of object permanence at different zoological levels. Hum Dev 27:309–320

Fahrig L, Rytwinski T (2009) Effects of roads on animal abundance: an empirical review and synthesis. Ecol Soc 14:1–20. doi: Artn 21

Fisher J, Hinde RA (1949) The opening of milk bottles by birds. Br Birds 42:347–357

Foltz SL, Ross AE, Laing BT, et al (2015) Get off my lawn: increased aggression in urban song sparrows is related to resource availability. Behav Ecol 26:1548–1557. doi: 10.1093/beheco/arv111

Forstmeier W, Nakagawa S, Griffith SC, Kempenaers B (2014) Female extra-pair mating: adaptation or genetic constraint? Trends Ecol Evol 29:456–464. doi: 10.1016/j.tree.2014.05.005

Freeberg TM (1999) Spatial Associations Provide a Context for Social Learning of Courtship Patterns in Brown-Headed Cowbirds (*Molothrus ater*). J Comp Psychol 113:327–332

Gao S, Sanchez C, Deviche PJ (2017) Corticosterone rapidly suppresses innate immune activity in the house sparrow (*Passer domesticus*). J Exp Biol 220:322–327. doi: 10.1242/jeb.144378

Garamszegi LZ, Eens M, Erritzøe J, Møller AP (2005) Sperm competition and sexually size dimorphic brains in birds. Proc R Soc B Biol Sci 272:159–166. doi: 10.1093/beheco/arh167

Garamszegi LZ, Erritzøe J, Møller AP (2007) Feeding innovations and parasitism in birds. Biol J Linn Soc 90:441–455

García-Navas V, Ferrer ES, Cáliz-Campal C, et al (2015) Spatiotemporal and genetic contingency of extrapair behaviour in a songbird. Anim Behav 106:157–169. doi: 10.1016/j.anbehav.2015.05.020

Geffroy B, Samia DSM, Bessa E, Blumstein DT (2015) How nature-based tourism might increase prey vulnerability to predators. Trends Ecol Evol 30:755–765. doi: 10.1016/j.tree.2015.09.010

Giraldeau L-A, Caraco T (2000) Social Foraging Theory. Princeton University Press, Princeton, New Jersey, U.S.A.

Giraldeau L-A, Caraco T, Valone TJ (1994) Social foraging: individual learning and cultural transmission of innovations. Behav Ecol 5:35–43

Giraldeau L-A, Lefebvre L (1987) Scrounging prevents cultural transmission of food-finding behaviour in pigeons. Anim Behav 35:387–394

Gizzi E, Castro MG, Sinapov J (2019) Creative problem solving by robots using action primitive discovery. In: 2019 Joint IEEE 9th International Conference on Development and Learning and Epigenetic Robotics (ICDL-EpiRob). IEEE, Oslo, pp 228–233

Grace JK, Froud L, Meillère A, Angelier F (2017) House sparrows mitigate growth effects of post-natal glucocorticoid exposure at the expense of longevity. Gen Comp Endocrinol 253:1–12. doi: 10.1016/j.ygcen.2017.08.011

Greenberg R (2003) The role of neophobia and neophilia in the development of innovative behaviour of birds. In: Reader SM, Laland KN (eds) Animal innovation. Oxford University Press, Oxford (NY), pp 175–196

Greggor AL, Thornton A, Clayton NS (2015) Neophobia is not only avoidance: improving neophobia tests by combining cognition and ecology. Curr Opin Behav Sci 6:82–89. doi: 10.1016/j.cobeha.2015.10.007

Greggor AL, Trimmer PC, Barrett BJ, Sih A (2019) Challenges of learning to escape evolutionary traps. Front Ecol Evol 7:408. doi: 10.3389/fevo.2019.00408

Griffin AS (2016) Innovativeness as an emergent property: a new alignment of comparative and experimental research on animal innovation. Philos Trans R Soc B Biol Sci 371:20150544. doi: 10.1098/rstb.2015.0544

Griffin AS, Diquelou M, Perea M (2014) Innovative problem solving in birds: a key role of motor diversity. Anim Behav 92:221–227. doi: 10.1016/j.anbehav.2014.04.009

Griffin AS, Guez D (2016) Bridging the gap between cross-taxon and within-species analyses of behavioral innovations in birds: making sense of discrepant cognition–innovation relationships and the role of motor diversity. In: Naguib M, Mitani JC, Simmons LW, et al. (eds) Advances in the Study of Behavior. Academic Press, pp 1–40

Griffin AS, Guez D (2014) Innovation and problem solving: A review of common mechanisms. Behav Processes 109:121–134. doi: 10.1016/j.beproc.2014.08.027

Griffin AS, Guez D, Lermite F, Patience M (2013a) Tracking changing environments: innovators are fast, but not flexible learners. PLoS One 8:e84907. doi: 10.1371/journal.pone.0084907

Griffin AS, Lermite F, Perea M, Guez D (2013b) To innovate or not: contrasting effects of social groupings on safe and risky foraging in Indian mynahs. Anim Behav 86:1291–1300. doi: 10.1016/j.anbehav.2013.09.035

Griffin AS, Netto K, Peneaux C (2017) Neophilia, innovation and learning in an urbanized world: a critical evaluation of mixed findings. Curr Opin Behav Sci 16:15–22. doi: 10.1016/j.cobeha.2017.01.004

Griffith SC, Owens IPF, Thuman K a. (2002) Extra pair paternity in birds: A review of interspecific variation and adaptive function. Mol Ecol 11:2195–2212. doi: 10.1046/j.1365-294X.2002.01613.x

Groothuis TGG, Carere C (2005) Avian personalities: characterization and epigenesis. Neurosci Biobehav Rev 29:137–150. doi: 10.1016/j.neubiorev.2004.06.010

Guez D, Griffin AS (2016) Unraveling the key to innovative problem solving: a test of learning versus persistence. Behav Ecol 27:1449–1460. doi: 10.1093/beheco/arw055

Hardy ICW, Briffa M (eds) (2013) Animal Contests, First. Cambridge University Press, New York

Harrison TJE, Smith JA, Martin GR, et al (2010) Does food supplementation really enhance productivity of breeding birds? Oecologia 164:311–320. doi: 10.1007/s00442-010-1645-x

Herborn KA, Macleod R, Miles WTS, et al (2010) Personality in captivity reflects personality in the wild. Anim Behav 79:835–843. doi: 10.1016/j.anbehav.2009.12.026

Hoi-Leitner M, Hoi H, Romero-Pujante M, Valera F (1999) Female extra-pair behaviour and environmental quality in the serin (*Serinus serinus*): a test of the `constrained female hypothesis'. Proc R Soc B Biol Sci 266:1021–1026. doi: 10.1098/rspb.1999.0738

Isden J, Panayi C, Dingle C, Madden JR (2013) Performance in cognitive and problem-solving tasks in male spotted bowerbirds does not correlate with mating success. Anim Behav 86:829–838. doi: 10.1016/j.anbehav.2013.07.024

Iyengar E V. (2008) Kleptoparasitic interactions throughout the animal kingdom and a re-evaluation, based on participant mobility, of the conditions promoting the evolution of kleptoparasitism. Biol J Linn Soc 93:745–762. doi: 10.1111/j.1095-8312.2008.00954.x

Johnson-Ulrich L, Benson-Amram S, Holekamp KE (2019) Fitness consequences of innovation in spotted hyenas. Front Ecol Evol 7:443. doi: 10.3389/fevo.2019.00443

Kalinowski ST, Taper ML, Marshall TC (2007) Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. Mol Ecol 16:1099–1106. doi: 10.1111/j.1365-294X.2007.03089.x

Kalinowski ST, Wagner AP, Taper ML (2006) ML-RELATE: a computer program for maximum likelihood estimation of relatedness and relationship. Mol Ecol Notes 6:576–579. doi: 10.1111/j.1471-8286.2006.01256.x

Katsnelson E, Motro U, Feldman MW, Lotem A (2011) Individual-learning ability predicts social-foraging strategy in house sparrows. Proc R Soc B Biol Sci 278:582–589. doi: 10.1098/rspb.2010.1151

Kawai M (1965) Newly-acquired pre-cultural behavior of the natural troop of japanese monkeys on Koshima Islet. Primates 6:1–30

Keagy J, Savard J-F, Borgia G (2011) Complex relationship between multiple measures of cognitive ability and male mating success in satin bowerbirds, *Ptilonorhynchus violaceus*. Anim Behav 81:1063–1070. doi: 10.1016/j.anbehav.2011.02.018

Keagy J, Savard J-F, Borgia G (2009) Male satin bowerbird problem-solving ability predicts mating success. Anim Behav 78:809–817. doi: 10.1016/j.anbehav.2009.07.011

Ketterson ED, King JR (1977) Metabolic and behavioral responses to fasting in the white-crowned sparrow (*Zonotrichia leucophrys gambelii*). Physiol Zool 50:115–129

Kimball RT (1996) Female choice for male morphological traits in house sparrows, *Passer domesticus*. Ethology 102:639–648. doi: 10.1111/j.1439-0310.1996.tb01155.x

Kotrschal A, Corral-Lopez A, Amcoff M, Kolm N (2015) A larger brain confers a benefit in a spatial mate search learning task in male guppies. Behav Ecol 26:527–532. doi: 10.1093/beheco/aru227

Kotrschal A, Rogell B, Bundsen A, et al (2013) Artificial selection on relative brain size in the guppy reveals costs and benefits of evolving a larger brain. Curr Biol 23:168–171. doi: 10.1016/j.cub.2012.11.058

Kozlovsky D, Branch C, Freas CA, Pravosudov V V. (2014) Elevation-related differences in novel environment exploration and social dominance in food-caching mountain chickadees. Behav Ecol Sociobiol 68:1871–1881. doi: 10.1007/s00265-014-1796-6

Kozlovsky DY, Branch CL, Pravosudov V V. (2015) Problem-solving ability and response to novelty in mountain chickadees (*Poecile gambeli*) from different elevations. Behav Ecol Sociobiol 635–643. doi: 10.1007/s00265-015-1874-4

Kozlovsky DY, Weissgerber EA, Pravosudov V V (2017) What makes specialized food-caching mountain chickadees successful city slickers? Proc R Soc B Biol Sci 284:20162613

Kriska G, Malik P, Szivák I, Horváth G (2008) Glass buildings on river banks as “polarized light traps” for mass-swarming polarotactic caddis flies. Naturwissenschaften 95:461–467. doi: 10.1007/s00114-008-0345-4

Krokene C, Rigstad K, Dale M, Lifjeld JT (1998) The function of extrapair paternity in blue tits and great tits: good genes or fertility insurance? Behav Ecol 9:649–656

Kummer H, Goodall J (1985) Conditions of innovative behaviour in primates. Philos Trans R Soc B Biol Sci 308:203–214

Laland KN, Reader SM (1999a) Foraging innovation is inversely related to competitive ability in male but not in female guppies. Behav Ecol 10:270–274

Laland KN, Reader SM (1999b) Foraging innovation in the guppy. Anim Behav 57:331–340. doi: 10.1006/anbe.1998.0967

Laucht S, Kempenaers B, Dale J (2010) Bill color, not badge size, indicates testosterone-related information in house sparrows. Behav Ecol Sociobiol 64:1461–1471. doi: 10.1007/s00265-010-0961-9

Lefebvre L (1995) The opening of milk bottles by birds: Evidence for accelerating learning rates, but against the wave-of-advance model of cultural transmission. Behav Processes 34:43–54

Lefebvre L, Reader SM, Sol D (2004) Brains, innovations and evolution in birds and primates. Brain Behav Evol 63:233–246. doi: 10.1159/000076784

Lendvai ÁZ, Barta Z, Liker A, Bókony V (2004) The effect of energy reserves on social foraging: hungry sparrows scrounge more. Proc R Soc B Biol Sci 271:2467–2472. doi: 10.1098/rspb.2004.2887

Lendvai ÁZ, Liker A, Barta Z (2006) The effects of energy reserves and dominance on the use of social-foraging strategies in the house sparrow. Anim Behav 72:747–752. doi: 10.1016/j.anbehav.2005.10.032

Liker A, Barta Z (2002) The effects of dominance on social foraging tactic use in house sparrows. Behaviour 139:1061–1076. doi: 10.1163/15685390260337903

Liker A, Barta Z (2001) Male badge size predicts dominance against females in House Sparrows. Condor 103:151–157. doi: 10.1650/0010-5422(2001)103[0151:MBSPDA]2.0.CO;2

Liker A, Bókony V (2009) Larger groups are more successful in innovative problem solving in house sparrows. Proc Natl Acad Sci U S A 106:7893–7898. doi: 10.1073/pnas.0900042106

López-Sepulcre A, Kokko H (2012) Understanding behavioural responses and their consequences. In: Candolin U, Wong BBM (eds) Behavioural responses to a changing world, First. Oxford University Press Inc., Oxford, United Kingdom, pp 3–15

Loss SR, Will T, Loss SS, Marra PP (2014) Bird–building collisions in the United States: Estimates of annual mortality and species vulnerability. Condor 116:8–23. doi: 10.1650/CONDOR-13-090.1

Lubjuhn T, Strohbach S, Brün J, et al (1999) Extra-pair paternity in great tits (*Parus major*) – a long term study. Behaviour 136:1157–1172

Madden JR (2007) Innovation in sexual display. Behav Brain Sci 30:417–418. doi: 10.1017/S0140525X07002488

Martin II LB (2005) Trade-offs between molt and immune activity in two populations of house sparrows (*Passer domesticus*). Can J Zool 83:780–787. doi: 10.1139/Z05-062

Martin II LB, Fitzgerald L (2005) A taste for novelty in invading house sparrows, Passer domesticus. Behav Ecol 16:702–707. doi: 10.1093/beheco/ari044

Mason GJ (2010) Species differences in responses to captivity : stress , welfare and the comparative method. Trends Ecol Evol 25:713–721. doi: 10.1016/j.tree.2010.08.011

Mateos-Gonzalez F, Quesada J, Senar JC (2011) Sexy birds are superior at solving a foraging problem. Biol Lett 7:668–669. doi: 10.1098/rsbl.2011.0163

McGraw KJ, Medina-Jerez W, Adams H (2007) Carotenoid-based plumage coloration and aggression during molt in male house finches. Behaviour 144:165–178. doi: 10.1163/156853907779947328

McKechnie AE, Freckleton RP, Jetz W (2006) Phenotypic plasticity in the scaling of avian basal metabolic rate. Proc R Soc B Biol Sci 273:931–937. doi: 10.1098/rspb.2005.3415

McKinney ML (2008) Effects of urbanization on species richness: A review of plants and animals. Urban Ecosyst 11:161–176. doi: 10.1007/s11252-007-0045-4

Milligan BG (2003) Maximum-likelihood estimation of relatedness. Genetics 163:1153–1167

Miranda AC (2017) Mechanisms of behavioural change in urban animals: the role of microevolution and phenotypic plasticity. In: Ecology and conservation of birds in urban environments. Springer, pp 113–132

Miranda AC, Schielzeth H, Sonntag T, Partecke J (2013) Urbanization and its effects on personality traits: a result of microevolution or phenotypic plasticity? Glob Chang Biol 19:2634–2644. doi: 10.1111/gcb.12258

Møller AP (1987) Variation in badge size in male house sparrows Passer domesticus : evidence for status signalling. Anim Behav 35:1637–1644

Moore JE, Wallace BP, Lewison RL, et al (2009) A review of marine mammal, sea turtle and seabird bycatch in USA fisheries and the role of policy in shaping management. Mar Policy 33:435–451. doi: 10.1016/j.marpol.2008.09.003

Morand-Ferron J, Cole EF, Quinn JL (2015) Studying the evolutionary ecology of cognition in the wild: a review of practical and conceptual challenges. Biol Rev Camb Philos Soc. doi: 10.1111/brv.12174

Morand-Ferron J, Quinn JL (2015) The evolution of cognition in natural populations. Trends Cogn Sci 1–3. doi: 10.1016/j.tics.2015.03.005

Morand-Ferron J, Quinn JL (2011) Larger groups of passerines are more efficient problem solvers in the wild. Proc Natl Acad Sci U S A 108:15898–15903. doi: 10.1073/pnas.1111560108

Morrell LJ, Lindström J, Ruxton GD (2005) Why are small males aggressive? Proc R Soc B Biol Sci 272:1235–41. doi: 10.1098/rspb.2005.3085

Mutzel A, Kempenaers B, Laucht S, et al (2011) Circulating testosterone levels do not affect exploration in house sparrows: Observational and experimental tests. Anim Behav 81:731–739. doi: 10.1016/j.anbehav.2011.01.001

Navarrete AF, Reader SM, Street SE, et al (2016) The coevolution of innovation and technical intelligence in primates. Philos Trans R Soc B Biol Sci 371:20150186. doi: 10.1098/rstb.2015.0186

Nemeth NM, Thomas NO, Orahood DS, et al (2010) Shedding and serologic responses following primary and secondary inoculation of house sparrows (Passer domesticus) and European starlings (*Sturnus vulgaris*) with low-pathogenicity avian influenza virus. Avian Pathol 39:411–418. doi: 10.1080/03079457.2010.513043

Nicol CJ, Pope SJ (1999) The effects of demonstrator social status and prior foraging success on social learning in laying hens. Anim Behav 57:163–171

Orizaola G, Dahl E, Laurila A (2012) Reversibility of predator-induced plasticity and its effect at a life-history switch point. Oikos 121:44–52. doi: 10.1111/j.1600-0706.2011.19050.x

Overington SE, Cauchard L, Côté K-A, Lefebvre L (2011a) Innovative foraging behaviour in birds: what characterizes an innovator? Behav Processes 87:274–85. doi: 10.1016/j.beproc.2011.06.002

Overington SE, Cauchard L, Morand-Ferron J, Lefebvre L (2009a) Innovation in groups: does the proximity of others facilitate or inhibit performance? Behaviour 146:1543–1564. doi: 10.1163/156853909X450131

Overington SE, Griffin AS, Sol D, Lefebvre L (2011b) Are innovative species ecological generalists? A test in North American birds. Behav Ecol 22:1286–1293. doi: 10.1093/beheco/arr130

Overington SE, Morand-Ferron J, Boogert NJ, Lefebvre L (2009b) Technical innovations drive the relationship between innovativeness and residual brain size in birds. Anim Behav 78:1001–1010. doi: 10.1016/j.anbehav.2009.06.033

Papp S, Vincze E, Preiszner B, et al (2015) A comparison of problem-solving success between urban and rural house sparrows. Behav Ecol Sociobiol 69:471–480. doi: 10.1007/s00265-014-1859-8

Patrick SC, Chapman JR, Dugdale HL, et al (2012) Promiscuity, paternity and personality in the great tit. Proc R Soc B Biol Sci 279:1724–1730. doi: 10.1098/rspb.2011.1820

Peakall R, Smouse PE (2012) GenAlEx 6.5: genetic analysis in Excel. Population genetic software for teaching and research — an update. Bioinformatics 28:2537–2539. doi: 10.1093/bioinformatics/bts460

Peig J, Green AJ (2009) New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. Oikos 118:1883–1891. doi: 10.1111/j.1600-0706.2009.17643.x

Pinheiro J, Bates D, DebRoy S, et al (2016) nlme: linear and nonlinear mixed effects models

Pipoly I, Szabó K, Bókony V, et al (2019) Higher frequency of extra-pair offspring in urban than forest broods of great tits (*Parus major*). Front Ecol Evol 7:1–5. doi: 10.3389/fevo.2019.00229

Plummer KE, Bearhop S, Leech DI, et al (2013) Winter food provisioning reduces future breeding performance in a wild bird. Sci Rep 3:2002. doi: 10.1038/srep02002

Poirier C, Henry L, Mathelier M, et al (2004) Direct social contacts override auditory information in the song-learning process in starlings (*Sturnus vulgaris*). J Comp Psychol 118:179–193

Pongrácz P, Vida V, Bánhegyi P, Miklósi A (2008) How does dominance rank status affect individual and social learning performance in the dog (*Canis familiaris*)? Anim Cogn 11:75–82. doi: 10.1007/s10071-007-0090-7

Pravosudov V V., Roth TC (2013) Cognitive ecology of food hoarding: The evolution of spatial memory and the hippocampus. Annu Rev Ecol Evol Syst 44:173–193. doi: 10.1146/annurev-ecolsys-110512-135904

Preiszner B, Papp S, Pipoly I, et al (2017) Problem-solving performance and reproductive success of great tits in urban and forest habitats. Anim Cogn 20:53–63. doi: 10.1007/s10071-016-1008-z

Preiszner B, Papp S, Vincze E, et al (2015) Does innovation success influence social interactions? An experimental test in house sparrows. Ethology 121:661–673. doi: 10.1111/eth.12380

Prokosch MD, Coss RG, Scheib JE, Blozis SA (2009) Intelligence and mate choice: intelligent men are always appealing. Evol Hum Behav 30:11–20. doi: 10.1016/j.evolhumbehav.2008.07.004

Quinn J, Cole E, Reed T, Morand-Ferron J (2016) Environmental and genetic determinants of innovativeness in a natural population of birds. Philos Trans R Soc B Biol Sci 371:20150184. doi: 10.1098/rstb.2015.0184

Quinn JL, Cole EF, Bates J, et al (2012) Personality predicts individual responsiveness to the risks of starvation and predation. Proc R Soc B Biol Sci 279:1919–1926. doi: 10.1098/rspb.2011.2227

R Core Team (2018) R: A Language and environment for statistical computing

R Development Core Team (2012) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Ramsey G, Bastian ML, van Schaik C (2007) Animal innovation defined and operationalized. Behav Brain Sci 30:393–407; discussion 407-432. doi: 10.1017/S0140525X07002373

Reader SM, Hager Y, Laland KN (2011) The evolution of primate general and cultural intelligence. Philos Trans R Soc B Biol Sci 366:1017–1027. doi: 10.1098/rstb.2010.0342

Reader SM, Laland KN (2003) Animal Innovation. Oxford University Press Inc., Oxford, New York, U.S.A.

Reader SM, Laland KN (2001) Primate innovation : sex , age and social rank differences. Int J Primatol 22:787–805

Reader SM, Morand-Ferron J, Flynn E (2016) Animal and human innovation: novel problems and novel solutions. Philos Trans R Soc B Biol Sci 371:20150182

Repka S, Pihlajamaa K (1996) Predator-induced phenotypic plasticity in *Daphnia pulex*: uncoupling morphological defenses and life history shifts. Hydrobiologia 339:67–71

Rousset F (2008) GENEPOP ' 007: a complete re-implementation of the GENEPOP software for Windows and Linux. Mol Ecol Resour 8:103–106. doi: 10.1111/j.1471-8286.2007.01931.x

Rowe C, Healy SD (2014) Measuring variation in cognition. Behav Ecol 25:1287–1292. doi: 10.1093/beheco/aru090

Rutte C, Taborsky M, Brinkhof MWG (2006) What sets the odds of winning and losing? Trends Ecol Evol 21:16–21. doi: 10.1016/j.tree.2005.10.014

Schlicht E, Kempenaers B (2015) Immediate effects of capture on nest visits of breeding blue tits, *Cyanistes caeruleus*, are substantial. Anim Behav 105:63–78. doi: 10.1016/j.anbehav.2015.04.010

Schuyler Q, Hardesty BD, Wilcox C, Townsend K (2014) Global analysis of anthropogenic debris ingestion by sea turtles. Conserv Biol 28:129–139. doi: 10.1111/cobi.12126

Schwabl H, Holmes D, Strasser R, Scheuerlein A (2012) Embryonic exposure to maternal testosterone influences age-specific mortality patterns in a captive passerine bird. Age (Omaha) 34:87–94. doi: 10.1007/s11357-011-9222-8

Seress G, Bókony V, Heszberger J, Liker A (2011) Response to predation risk in urban and rural house sparrows. Ethology 117:896–907. doi: 10.1111/j.1439-0310.2011.01944.x

Seress G, Bókony V, Pipoly I, et al (2012) Urbanization, nestling growth and reproductive success in a moderately declining house sparrow population. J Avian Biol 43:403–414. doi: 10.1111/j.1600-048X.2012.05527.x

Seress G, Hammer T, Bókony V, et al (2018) Impact of urbanization on abundance and phenology of caterpillars and consequences for breeding in an insectivorous bird. Ecol Appl 28:1143-1156. doi: 10.1002/eap.1730

Seress G, Liker A (2015) Habitat urbanization and its effects on birds. Acta Zool Acad Sci Hungaricae 61:373–408. doi: 10.17109/AZH.61.4.373.2015

Shettleworth SJ (2010) Cognition, Evolution, and Behaviour, Second. Oxford University Press, New York

Shochat E, Warren PS, Faeth SH, et al (2006) From patterns to emerging processes in mechanistic urban ecology. Trends Ecol Evol 21:186–91. doi: 10.1016/j.tree.2005.11.019

Simons MJP, Winney I, Girndt A, et al (2019) Ageing in house sparrows is insensitive to environmental effects. bioRxiv 1–31. doi: 10.1101/598284

Slagsvold T, Lifjeld JT (1997) Incomplete female knowledge of male quality may explain variation in extra-pair paternity in birds. Behaviour 134:353–371

Smallwood KS (2013) Comparing bird and bat fatality-rate estimates among North American wind-energy projects. Wildl Soc Bull 37:19–33. doi: 10.1002/wsb.260

Sol D, Griffin AS, Bartomeus I (2012) Consumer and motor innovation in the common myna: the role of motivation and emotional responses. Anim Behav 83:179–188. doi: 10.1016/j.anbehav.2011.10.024

Sol D, Griffin AS, Bartomeus I, Boyce H (2011) Exploring or avoiding novel food resources? The novelty conflict in an invasive bird. PLoS One 6:e19535. doi: 10.1371/journal.pone.0019535

Sol D, Lapiedra O, González-Lagos C (2013) Behavioural adjustments for a life in the city. Anim Behav 85:1101–1112. doi: 10.1016/j.anbehav.2013.01.023

Sol D, Lefebvre L, Rodríguez-Teijeiro JD (2005) Brain size, innovative propensity and migratory behaviour in temperate Palaearctic birds. Proc R Soc B Biol Sci 272:1433–1441. doi: 10.1098/rspb.2005.3099

Sol D, Sayol F, Ducatez S, Lefebvre L (2016) The life-history basis of behavioural innovations. Philos Trans R Soc B Biol Sci 371:20150187

Sol D, Timmermans S, Lefebvre L (2002) Behavioural flexibility and invasion success in birds. Anim Behav 63:495–502. doi: 10.1006/anbe.2001.1953

Solonen T (2001) Breeding of the Great Tit and Blue Tit in urban and rural habitats in southern Finland. Ornis Fenn 78:49–60

Sonnenberg BR, Branch CL, Pitera AM, et al (2019) Natural selection and spatial cognition in wild food- caching mountain chickadees. Curr Biol 29:670–676. doi: 10.1016/j.cub.2019.01.006

Stevens JR, Gilby IC (2004) A conceptual framework for nonkin food sharing: timing and currency of benefits. Anim Behav 67:603–614. doi: 10.1016/j.anbehav.2003.04.012

Strohbach S, Curio E, Bathen A, et al (1998) Extrapair paternity in the great tit (*Parus major*): a test of the “good genes” hypothesis. Behav Ecol 9:388–396

Stuebe MM, Ketterson ED (1982) A study of fasting in tree sparrows (*Spizella arborea*) and dark-eyed juncos (*Junco hyemalis*): ecological implications. Am Nat 99:299–308

Suárez-Rodríguez M, Garcia M (2014) There is no such a thing as a free cigarette; lining nests with discarded butts brings short-term benefits, but causes toxic damage. J Evol Biol 27:2719–2726. doi: 10.1111/jeb.12531

Suárez-Rodríguez M, López-Rull I, Garcia CM (2013) Incorporation of cigarette butts into nests reduces nest ectoparasite load in urban birds: new ingredients for an old recipe? Biol Lett 9:9–12

Svensson L (1992) Identification Guide to European Passerines, Fourth. BTO, Stockholm, Sweden

Tang YP, Shimizu E, Dube GR, et al (1999) Genetic enhancement of learning and memory in mice. Nature 401:63–69

Tebbich S, Griffin AS, Peschl MF, Sterelny K (2016) From mechanisms to function: an integrated framework of animal innovation. Philos Trans R Soc B Biol Sci 371:20150195

Thornton A, Isden J, Madden JR (2014) Toward wild psychometrics: linking individual cognitive differences to fitness. Behav Ecol 25:1299–1301. doi: 10.1093/beheco/aru095

Thornton A, Lukas D (2012) Individual variation in cognitive performance : developmental and evolutionary perspectives. Philos Trans R Soc B Biol Sci 367:2773–2783. doi: 10.1098/rstb.2012.0214

Thornton A, Samson J (2012) Innovative problem solving in wild meerkats. Anim Behav 83:1459–1468. doi: 10.1016/j.anbehav.2012.03.018

Tóth Z, Bókony V, Lendvai ÁZ, et al (2009a) Effects of relatedness on social-foraging tactic use in house sparrows. Anim Behav 77:337–342. doi: 10.1016/j.anbehav.2008.10.005

Tóth Z, Bókony V, Lendvai ÁZ, et al (2009b) Whom do the sparrows follow? The effect of kinship on social preference in house sparrow flocks. Behav Processes 82:173–177. doi: 10.1016/j.beproc.2009.06.003

Tóth Z, Bókony V, Lendvai ÁZ, et al (2009c) Kinship and aggression: do house sparrows spare their relatives? Behav Ecol Sociobiol 63:1189–1196. doi: 10.1007/s00265-009-0768-8

Tryjanowski P, Skórka P, Sparks TH, et al (2015) Urban and rural habitats differ in number and type of bird feeders and in bird species consuming supplementary food. Environ Sci Pollut Res 22:15097–15103. doi: 10.1007/s11356-015-4723-0

Van Buskirk J (2012) Behavioural plasticity and environmental change. In: Candolin U, Wong BBM (eds) Behavioural responses to a changing world, First. Oxford University Press Inc., Oxford, United Kingdom, pp 145–158

van Oers K, Drent PJ, Dingemanse NJ, Kempenaers B (2008) Personality is associated with extrapair paternity in great tits, Parus major. Anim Behav 76:555–563. doi: 10.1016/j.anbehav.2008.03.011

Van Oosterhout C, Hutchinson WF, Wills DP, Shipley P (2004) MICRO - CHECKER: software for identifying and correcting genotyping errors in microsatellite data. Mol Ecol Notes 4:535–538. doi: 10.1111/j.1471-8286.2004.00684.x

Vas Z, Lefebvre L, Johnson KP, et al (2011) Clever birds are lousy: co-variation between avian innovation and the taxonomic richness of their amblyceran lice. Int J Parasitol 41:1295–300. doi: 10.1016/j.ijpara.2011.07.011

Verboven N, Mateman AC (1997) Low frequency of extra-pair fertilizations in the great tit *Parus major* revealed by DNA fingerprinting. J Avian Biol 28:231–239

Vincze E, Papp S, Preiszner B, et al (2016) Habituation to human disturbance is faster in urban than rural house sparrows. Behav Ecol 27:1304–1313. doi: 10.1093/beheco/arw047

Vincze E, Papp S, Preiszner B, et al (2015) Does urbanization facilitate individual recognition of humans by house sparrows? Anim Cogn 18:291–298. doi:10.1007/s10071-014-0799-z

Wan D, Peng C, Jiangxia Y (2013) Causes of extra-pair paternity and its inter-specific variation in socially monogamous birds. Acta Ecol Sin 33:158–166. doi: 10.1016/j.chnaes.2013.03.006

Wascher CAF, Kulahci IG, Langley EJG, Shaw RC (2018) How does cognition shape social relationships? Philos Trans R Soc B Biol Sci 373:20170293

West-Eberhard MJ (1989) Phenotypic plasticity and the origins of diversity. Annu Rev Ecol Syst 20:249–278

West RJD (2014) The evolution of large brain size in birds is related to social, not genetic, monogamy. Biol J Linn Soc 111:668–678. doi: 10.1111/bij.12193

Westneat DF, Stewart IRK (2003) Extra-pair paternity in birds: causes, correlates, and conflict. Annu Rev Ecol Evol Syst 34:365–396. doi: 10.1146/132439

Wetzel DP (2017) Problem-solving skills are linked to parental care and offspring survival in wild house sparrows. Ethology 123:475–483. doi: 10.1111/eth.12618

While GM, Sinn DL, Wapstra E (2009) Female aggression predicts mode of paternity acquisition in a social lizard. Proc R Soc B Biol Sci 276:2021–2029. doi: 10.1098/rspb.2008.1926

Whittingham LA, Dunn PO (2001) Male parental care and paternity in birds. In: Nolan V, Thompson CF (eds) Current Ornithology. Springer US, Boston, MA, pp 257–298

Wiley RH (1991) Both high- and low-ranking white-throated sparrows find novel locations of food. Auk 108:8–15

Yong-Kyu K (2009) Handbook of behavior genetics. Springer US, New York