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Behavioral responses to humans and predators in urban and non-urban birds

PhD thesis

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BEHAVIORAL RESPONSES TO HUMANS AND PREDATORS IN URBAN AND NON-URBAN BIRDS

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CONTENTS

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ABSTRACT (IN ENGLISH)

Urban habitats differ from non-urban habitats in many environmental characteristics, including the population density of humans and various forms of anthropogenic disturbance, as well as the composition of the predator fauna and, potentially, the predation risk they pose on their prey. These ecological differences, in turn, can lead to differences between urban and non-urban populations of animals in their behavior towards humans and non-human predators. The aim of present thesis was to investigate differences between urban and non-urban populations of two bird species, the house sparrow (*Passer domesticus*) and the great tit (*Parus major*), in their responses to potentially dangerous and non-dangerous humans, as well as a natural predator, the sparrowhawk (*Accipiter nisus*). Furthermore, in a meta-analysis, I explored whether predation rate on natural and artificial bird nests differs between urban and non-urban habitats. In house sparrows, I found that birds in urban habitats had shorter flight initiation distances from humans than birds in rural habitats such as farmlands. In captivity, urban and non-urban sparrows showed similar initial fear response to human disturbance, but urban sparrows habituated faster to repeated disturbance. Furthermore, following repeated encounters with a hostile and a non-hostile person in captivity, rural sparrows became less fearful from the non-hostile person compared to the hostile or an unfamiliar person, but urban sparrows made no such distinction. Similarly to sparrows, great tits breeding in artificial nest boxes responded less fearfully to human disturbance in urban than in non-urban (forest) habitats, but neither urban nor non-urban great tits differentiated between an unfamiliar and a familiar, previously hostile person. Urban great tits also responded less fearfully to sparrowhawk than non-urban great tits, but there was no correlation between the response to human disturbance and the response to sparrowhawk. The meta-analysis showed that natural bird nests were less predated in urban than in rural habitats, but artificial bird nests were more predated in cities. These results, overall, imply that urban birds are generally less fearful from humans than non-urban birds; this, at least partly, is likely due to faster habituation to humans by urban birds. Distinguishing between differently dangerous humans is not general among birds, but may be the most advantageous in moderately anthropogenic habitats such as farmlands, possibly because of the relatively frequent repeated encounters with the same persons and/or the more frequent hostile behavior of humans towards birds in these habitats. Less fearful behavior towards sparrowhawk by urban great tits is unlikely to be connected to behavior towards humans, and instead likely to be either due to environmental constraints and/or lower predation risk in urban habitats. Lower mortality of natural bird nests in urban habitats also suggests lower

predation pressure in cities, but this is contrasted by higher mortality of artificial nests in cities. Taken together, I conclude that urbanization changes predator-prey relationships and behavior towards humans and non-human predators in a complex and context-dependent way.

KIVONAT (MAGYARUL)

A városi élőhelyek számos környezeti tényezőben különböznek a természetes élőhelyektől, többek között nagyszámú ember és sokféle emberi zavarás jellemzi őket. Emellett a városi és természetes élőhelyek közt eltérhet a ragadozó-fauna és az általuk jelentett predációs kockázat is. Ezen ökológiai különbségek hatására eltérések alakulhatnak ki a városi és a nem urbanizált állatpopulációk között az emberrel és nem emberi ragadozókkal szembeni viselkedésükben. Disszertációm célja, hogy összehasonlítsam két madárfaj, a házi veréb (*Passer domesticus*) és a széncinege (*Parus major*) városi és nem urbanizált populációi között a veszélyes és nem veszélyes emberekkel, illetve természetes ragadozójukkal, a karvallyal (*Accipiter nisus*) szembeni viselkedési válaszokat. Emellett metaanalízis segítségével megvizsgáltam, hogy a természetes, illetve mesterséges madárfészkek predációs rátája eltér-e városi és kevésbé urbanizált élőhelyek közt. A házi verebeknél azt találtam, hogy a madarak menekülési távolsága rövidebb volt városban, mint vidéki élőhelyeken (falvak szélén, tanyákon). Fogságban a városi és vidéki verebek első alkalommal egyformán reagáltak egy újfajta emberi zavarásra, de az ismételt zavaráshoz a városiak gyorsabban habituálódtak. Továbbá egy ellenséges és egy nem ellenséges emberrel való ismételt találkozásokat követően a vidéki verebek kevésbé féltek az utóbbitól, mint az előbbitől vagy egy ismeretlen személytől, míg a városiak nem tettek ilyen különbséget. A verebekhez hasonlóan a mesterséges odúkban fészkelő széncinegék is kevésbé féltek az embertől városban, mint nem urbanizált (erdei) élőhelyeken, ám sem a városi, sem az erdei cinegék nem tettek különbséget az ismeretlen és az ismerős, ellenséges ember közt. Emellett a városi széncinegék gyengébb félelmi választ mutattak karvalyra, mint az erdei széncinegék, ám a karvalyra és az emberre adott válaszuk nem korrelált egymással. A metaanalízis során azt találtam, hogy a természetes madárfészkek ritkábban estek zsákmányul városi, mint nem urbanizált élőhelyeken, míg a mesterséges fészkek predációja városban volt gyakoribb. Összességében az eredmények alapján úgy tűnik, hogy a városi madarak kevésbé félnek az embertől, mint nem urbanizált fajtársaik; ez valószínűleg, legalább részben, a városi egyedek gyorsabb habituációjával magyarázható. A különböző veszélyt jelentő emberek megkülönböztetése nem általánosan elterjedt a madarak közt, de leginkább falvak szélén, tanyákon lehet előnyös, mivel ezeken a helyeken gyakoribb lehet az ugyanazon személlyel való ismételt találkozás és/vagy az emberek madarakkal szembeni ellenséges viselkedése. A városi széncinegék karvallyal szembeni bátrabb viselkedése feltehetőleg nincs kapcsolatban az emberrel mutatott válasszal, hanem valamilyen környezeti kényszer és/vagy alacsonyabb predációs kockázat következménye. A városi természetes fészkek kisebb mortalitása szintén

arra utal, hogy az urbanizált élőhelyeken kisebb a predációs nyomás, de ennek ellentmond a mesterséges fészkek nagyobb mortalitása. A fentiek alapján arra következtetek, hogy az urbanizáció hatása a ragadozó-préda kapcsolatokra és az emberekkel és nem emberi ragadozókkal szembeni viselkedésre összetett és függ a vizsgált rendszertől.

RESUMEN (EN ESPAÑOL)

Hábitats urbanos son diferentes que hábitats naturales en características numerosas, como la población de humanos y formas variosas de disturbancia antropogenico, así como la composición de la fauna des predadores y el riesgo de depredación. A su vez, estas diferencias ecologicas pueden resultar en diferencias entre animales urbanos y non-urbanos en sus comportamientos para con humanos y predadores non-humanos. El objecto de esta tesis doctoral era la investigación de las diferencias entre poblaciones urbanos y non-urbanos de dos especies aviarios, el gorrión común (*Passer domesticus*) y el carbonero común (*Parus major*), en sus respuestas a humanos peligrosos y inofensivos, también un predador natural, el gavilán común (*Accipiter nisus*). Además, llevaba a cabo un metaanálisis, para investigar que depredación des nidos aviarios naturales y artificiales son diferentes en hábitats urbanos y non-urbanos. He descubierto que gorriónes urbanos tenían distancias de iniciación de huida más cortas que gorriónes de hábitats rústicos. En cautividad, respuestas iniciales de miedo a molestia humana des gorriónes urbanos y rústicos fuen similar, pero habituación a molestia repetida des gorriónes urbanos fue más rápido que gorriónes rústicos. Además, despues encuentros repetidos con un humano peligroso y un humano inofensivo, gorriónes rústicos fuen menos aprensivos del humano inofensivo que el humano peligroso y un humano desconosido, pero gorriónes urbanos no diferenciaban. Asimismo que gorriónes, carboneros que procreaban en cascados de nido respondieron con menos miedo a humanos en hábitats urbanos que en bosques. Sin embargo, carboneros de ningún hábitat diferenciaban entre un humano unfamiliar y un humano familiar y anteriormente peligroso. Carboneros urbanos respondieron con menos miedo también al gavilán que carboneros selváticos, pero había no correlación entre respuestas a humanos y respuestas al gavilán. El metaanálisis translucía que nidos naturales fuen depredados menos veces en hábitats urbanos que hábitats non-urbanos, pero nidos artificiales fuen depredados más veces en hábitats urbanos. En conjunto, estos resultados implican que pájaros urbanos son menos aprensivos a humanos que pájaros non-urbanos; como mínimo en parte, esto es en razón del habituación más rápido des pájaros urbanos. Diferenciar entre humanos diferentemente peligrosos no es generalizado entre pájaros, pero puede ser de más ventaja en hábitats moderadamente antropogénicos, posiblemente porque encuentros repetidos con los mismos humanos y/o animosidad de humanos a pájaros son más frecuentes en hábitats rústicos. Menos miedo a gavilán des carboneros urbanos es improbable que estar relacionado con comportamiento para humanos. En cambio, es probable que ser en razón de limitaciónes ambientales y/o menos riesgo de depredación. Menos mortalidad des nidos naturales en hábitats

urbanos también indica menos riesgo de depredación, pero esto es contraponiendo a más mortalidad des nidos artificiales en ciudades. Como conclusión, urbanización modifica relación de predador y presa, así como comportamiento para con humanos y predadores non-humanos, de una manera compleja y dependiente a contexto.

CHAPTER 1

GENERAL INTRODUCTION

1.1. Effects of urbanization on animal behavior

Urbanization, i.e. the expansion and development of cities as well as suburban and exurban areas, has reached a previously unseen extent in the last few decades (Angel et al. 2011). With the human population constantly growing, more and more natural habitats undergo anthropogenic changes, of which urbanization is one of the strongest. Urban habitats are characterized by altered landscapes such as reduced vegetation and large surfaces covered by concrete, altered flora with fewer native and more exotic species, higher level of chemical, noise and light pollution, climate differences (such as the "urban heat island effect"), and high density of the human population (Seress and Liker 2015). Many animal species establish themselves in urban habitats, either because they remain in their original habitat which undergoes urban development, or because they migrate there from other habitats.

The differences between natural and urbanized habitats have numerous ecological effects on the animals in urban areas (Ditchkoff et al. 2006; Sol et al. 2013; Seress and Liker 2015; Macías Garcia et al. 2017). Many of these effects (such as collisions with buildings and cars, various forms of pollution) are negative and result in reduced survival and reproduction. However, some of the effects can be beneficial, allowing certain species to thrive in urban habitats. Some species seem to be inherently better than others at establishing themselves in urban habitats, thanks to exaptations that were advantageous both in their original habitats and the novel habitat types (Sol et al. 2013). For example, a generalist and/or herbivorous diet (Evans et al. 2011), larger brain size (Carrete and Tella 2011; Maklakov et al. 2011; Snell-rood and Wick 2013) and small or medium body size (Bateman and Fleming 2012; Møller 2012) can all result in higher success in urban habitats in certain taxa. However, once a species successfully establishes itself in an urban habitat, urban and non-urban populations of the same species may show significant phenotypic differences. For example, urban birds typically start breeding on earlier dates and lay smaller clutches than rural birds (Chamberlain et al. 2009; Sprau et al. 2016). Male birds change their singing behavior, producing shorter and faster songs on higher frequencies to produce an effective signal in urban noise (Slabbekoorn and den Boer-Visser 2006). There are also differences between urban and rural populations of animals in behavioral traits like neophobia and neophilia (Miranda et al. 2013; Carrete and Tella 2017), aggressiveness (Scales et al. 2011; Møller and Ibáñez-Álamo 2012; Myers and Hyman 2016), and skills potentially related to cognition, such as innovation and problem solving (Audet et al. 2015; Papp et al. 2015; Preiszner et al. 2017), although the literature on whether and how these traits differ between urban and rural animals is often controversial, indicating that the effects are complex and dependent on species and conditions (Miranda 2017).

The above phenotypic differences between urban and rural populations of the same species can arise through a number of mechanisms: they may be. due to genetic, epigenetic or maternal effects (henceforth referred to as “intrinsic” differences), or could be the result of individual phenotypic plasticity (Miranda et al. 2013; Miranda 2017). Intrinsic differences between the populations can appear two different ways. When there is high phenotypic variation in the original population, individuals with the phenotype most suitable to urban conditions can establish themselves in cities, whereas less suitable individuals can remain in their original habitat (differential colonization or pre-colonization adaptation). Alternatively, when a population of animals colonizes a city, or their habitat undergoes urban transformation, the novel environmental conditions can induce local micro-evolutionary changes by natural selection, changing the genetic composition of the urban population (post-colonization adaptation). Some studies revealed differences between urban and rural populations in behavior-related candidate genes (Mueller et al. 2013; van Dongen et al. 2015), indicating that there are at least some major intrinsic differences.

In contrast, phenotypic plasticity on the individual level can also explain differences between habitats. Environmental effects (such as various forms of stress) that the animals experience during their life can affect their development, morphology, physiology and behavior. Phenotypic plasticity can be adaptive, as the animals can increase their fitness by adjusting their phenotype to what is optimal in their environment. However, in unfavorable environmental conditions, plasticity can also lead to disadvantageous phenotypic changes; for example, poor diet can lead to reduced cognitive abilities (Arnold et al. 2007). Changes due to phenotypic plasticity can happen over different time scales. Developmental plasticity, happening on the longest time scale, makes individuals of the same genotype developing different phenotypes over their lifetime, often irreversibly (and thus is not possible to distinguish from other, intrinsic differences by simply looking at the adults’ behavior). Learning processes like habituation, sensitization and operative problem solving happen over a somewhat shorter time scale, during repeated encounters of the same stimulus, and are often reversible. Behavioral flexibility means that an animal adjusts its behavior to a novel condition quickly (often upon the first encounter with the stimulus). Urban habitats are full of novel environmental factors that are less predictable in some aspects (e.g. rapid urban development) but more predictable in others (e.g. daily routines, reduced seasonal effects), compared to rural habitats (Griffin et al. 2017). Unpredictably changing environmental factors may favor short-term behavioral flexibility, whereas novel, but predictable factors may facilitate longer-term learning (Griffin et al. 2017). Therefore, both flexibility and learning are often believed to be advantageous in these habitats, although evidence for this is equivocal (Papp et al. 2015; Griffin et al. 2017; Miranda 2017). Plasticity and selection for intrinsic differences are non-exclusive: difference in phenotypes between urban and rural habitats is most likely a cumulative effect of the two. Furthermore, the capacity for behavioral plasticity may also be genetically determined; thus, there may be micro-evolutionary selection favoring individuals with greater habituation capacity, better learning abilities or more flexible behavior.

The relative importance of urban-rural phenotypic differences that are intrinsic and those that are due to plasticity is disputed. A meta-analysis showed that phenotypic morphological and life-history differences between wild-caught populations from habitats with different anthropogenic disturbance are seldom present in common garden and quantitative genetic experiments, which indicates that phenotypic plasticity is more important for these traits than intrinsic differences between populations. However, common garden studies investigating behavioral traits found that birds captured as nestlings from urban and rural habitats significantly differed in their neophobia and neophilia (Miranda et al. 2013), their exploratory behavior (Atwell et al. 2012) and their sedentariness (Partecke and Gwinner 2007), indicating intrinsic differences (due to genetic and/or maternal effects) at least in these traits. Studies investigating behavioral reaction norms, i.e. comparing within-individual variation with between-individual variation of a certain behavior (Dingemanse et al. 2010), also found that urban birds did not adjust their behavior to environmental conditions (i.e. human disturbance); instead, they showed behavioral consistency, and chose habitats with environmental conditions best fitting their behavioral type (Holtmann et al. 2017; Sprau and Dingemanse 2017). These results support the importance of intrinsic differences and/or developmental plasticity rather than behavioral flexibility.

Behaviors may show covariance across contexts, a phenomenon often referred to as behavioral syndrome (Sih et al. 2004a; Sih et al. 2004b; Sih and Bell 2008). For example, animals that flee from humans from greater distances may also show greater avoidance of novel objects (Carrete and Tella 2017), or birds that are aggressive towards conspecifics may also show more aggressive behavior towards predators (Myers and Hyman 2016). Such behavioral covariance can arise several ways: it can be the result of the same proximate (e.g. genetic, physiological and cognitive) regulating processes influencing the two types of behavior, or it can appear if the animal optimizes its behaviors independently to covarying environmental factors. Covariance between behaviors can be advantageous if a certain behavioral type increases success across contexts, but can also be disadvantageous if there is a trade-off across contexts (Sih and Bell 2008); this latter case is called “behavioral spillover” (Sih et al. 2004b). For example, an animal that behaves aggressively in different contexts can be more successful both in hunting prey and in competing with conspecifics, but there may be a behavioral spillover if too much aggression towards potential mates leads to lower breeding success (Sih et al. 2004a). When a species colonizes a novel habitat such as a city, it may encounter environmental conditions that do not necessarily covary the same way as in the original habitat. Therefore, a behavioral syndrome that was adaptive in the original habitat may be maladaptive in a novel habitat. This may lead to the behavioral syndromes “breaking down” in novel habitats: for example, behaviors that correlate in natural habitats may no longer show correlation in an urban habitat (Scales et al. 2011; Myers and Hyman 2016; Carrete and Tella 2017), either through behavioral plasticity or through intrinsic changes.

1.2.Urbanization and human-animal interactions

Urban habitats are, by definition, characterized by high density of human population. The interactions between humans and other animals found in urban habitats are multi-faceted. The majority of wild animals view humans as potential threat, and respond to an approaching human with flight (Frid and Dill 2002). This response has a strong basis in the animals’ evolutionary history, as many species have been hunted by humans for sport, food, or as a form of pest control for centuries or millennia. However, such hostile attitude towards animals is less common in cities; for example, one study showed that both hostile and friendly attitudes towards birds (i.e. people discouraging or encouraging birds to visit their homes and yards) are less common in urban than in rural areas (Clucas and Marzluff 2012). The antipredator behaviors that animals may show towards humans, like vigilance, escape and mobbing, are costly, as they are in trade-off with other, beneficial behaviors such as feeding or parental care, and thus may result in starvation of adults and offspring (Lima 1998). Furthermore, an animal showing mobbing behavior risks potential injury and even death (Sordahl 1990; Tórrez et al. 2012), and chronic fear can have negative physiological consequences (Clinchy et al. 2013). Therefore, as humans are extremely abundant but generally non-dangerous towards urban animals, an overall increased tolerance towards humans is advantageous.

In the upcoming chapters, I refer to behavioral responses to humans and other threatening stimuli as “fear responses”, “fearful behavior”, “boldness” and “risk taking”. The term “fear” can refer to a cognitive state (emotion), a physiological state, or to behavioral forms associated with these (Beauchamp 2017). “Boldness” is a term mostly used in animal personality research, often as a “boldness-shyness” personality dimension, indicating whether an animal consistently shows fearful (shy) or non-fearful (bold) behavior (Wilson et al. 1994). Finally, “risk taking” indicates an animal’s decision-making strategy in a dangerous situation, based on fitness benefits and costs of flight (Lima and Dill 1990). However, I am only looking at behavioral responses in my empirical studies, and only infer the animals’ physiological and cognitive state as well as the fitness benefits and costs of the behavior indirectly. Therefore I am using the above terms synonymously: if an animal responds to a potentially threatening stimulus with strong avoidance (such as flight or hiding), I consider it more fearful / less bold / less risk-taking than those who respond with weaker avoidance.

Responses to humans, like any other behavior, can differ between populations due to intrinsic differences between individuals (as result of mechanisms such as differential colonization or local adaptation), but also can be shaped by individual plasticity over lifetime. Animals can respond to repeated stress (such as repeated disturbance by humans) with two forms of plasticity: habituation and sensitization. Habituation means that if an animal is exposed to a stressful stimulus repeatedly, the intensity of its response decreases over repeated encounters, but not due to sensory or motoric fatigue (Rankin et al. 2009). Conversely, sensitization means an increased response towards the repeated stressful stimulus. Whether an animal habituates or sensitizes to a stressful stimulus primarily depends on the costs of responding versus not responding to it. If not responding to the stimulus has higher costs than responding (i.e. the stimulus indicates danger), then sensitization occurs, whereas in reverse cases (i.e. when the stimulus is relatively harmless), the animal will habituate to the stimulus. Urban humans are generally non-hostile towards birds (Clucas and Marzluff 2012), therefore habituation is more likely to happen. Habituation or sensitization can happen to any modality of the response, such as its magnitude, frequency, or duration (Rankin et al. 2009). For example, when habituating to humans, birds can reduce either the intensity of their reactions to humans (magnitude) or the time it takes for them to recover and return to their previous behavior after getting startled (duration). Fear responses to humans (most often measured by the flight initiation distance (FID), i.e. the distance from which an animal flees from an approaching threat such as a human) are generally lower in urban than in rural habitats (Samia et al. 2015), which is in line with the habituation hypothesis. However, it can also be explained by other mechanisms, such as pre-colonization or post-colonization adaptations resulting in intrinsic differences; little is known about the relative importance of these mechanisms.

Furthermore, animals can also benefit from humans. For example, people may provide food subsidies to animals (Rodewald et al. 2011a), either unintentionally, i.e. by leaving leftovers behind, or intentionally, i.e. via bird feeders (Møller et al. 2015; Reynolds et al. 2017). As natural sources of food (such as native plants and insects) are less common in urban habitats (McKinney 2006), urban animals may rely more on anthropogenic food subsidies (Rodewald et al. 2011a). Furthermore, humans can also provide shelter and breeding locations for animals (Tella et al. 2014). Another potential advantage of human presence to wild animals is proposed by the "human shield" hypothesis: the pressure from predation (and competition) may decrease for human-tolerant species if their predators (and/or competitors) are less tolerant towards anthropogenic disturbance and thus are less abundant in urban habitats (Møller 2012).

Due to individual humans having different attitudes towards birds, the ability to differentiate between potentially dangerous, neutral, and benevolent humans can be a major advantage for animals living in anthropogenic habitats. Recognizing humans who consistently behave in a hostile or benevolent way may be adaptive; for example, approaching benevolent humans who may provide food can increase foraging efficiency, and costly anti-predator behaviors such as mobbing can be focused only on hostile persons. In line with these expectations, the ability to recognize individual humans has been found in a number of birds species in anthropogenic habitats (Levey et al. 2009; Marzluff et al. 2010; Belguermi et al. 2011; Lee et al. 2011). However, so far it has never been tested whether urban or non-urban animals are better at recognizing people.

1.3. Urbanization and predator-prey interactions

Species on all trophic levels are likely to be affected by the various environmental factors that characterize urbanization. As not all species respond to urbanization in the same way, interspecific relationships, such as predator-prey relationships, can severely change along the urbanization gradient. Some predators seem to be sensitive to urbanization and thus less common in urban than in rural habitats, such as snakes (Patten and Bolger 2003), small and large mammalian predators (Bateman and Fleming 2012), and several species of raptors (Møller 2012). In contrast, opportunistic mesopredators, both birds (Jerzak 1997; Marzluff and Neatherlin 2006; Kövér et al. 2015) and mammals (Baker et al. 2001; Haskell et al. 2001; Prange and Gehrt 2004), can reach higher abundances in urbanized areas than in the surrounding rural matrix. Generally, medium-sized, generalist predators are more successful in cities, whereas larger, specialist predators are either declining or completely absent from such habitats (Bateman and Fleming 2012; Macías Garcia et al. 2017). Domestic cats (*Felis silvestris catus*) are also common in cities, with their abundance increasing with housing density (Sims et al. 2008), and are responsible for a significant mortality of both birds (including eggs) and other small vertebrates (Beckerman et al. 2007; Baker et al. 2008; Bonnington et al. 2013). Dogs (*Canis lupus familiaris*), while may seldom hunt for wild prey, are also seen by small animals as potential predators (Banks and Bryant 2007; Cavalli et al. 2016), thus their high abundance in cities can also increase the perceived predation risk.

This altered predator fauna may affect prey species in a complex way. Not only are different prey species likely to be affected differently, but predation pressure on prey can also change over its lifetime. Adult animals are mostly threatened by specialized, hyper-carnivorous predators, whereas opportunistic predators are likely to pose a bigger threat to eggs and juveniles. As nests are sedentary and thus much easier to monitor than adult animals, most studies that investigated predation in the context of urbanization focused on the survival of bird nests.

One approach to investigate predators' effect on prey is to look at prey mortality due to predation. Studies using this approach have been largely controversial. Some studies reported higher prey mortality (particularly nest mortality) in urban than in non-urban habitats, supported by surveys finding more potential nest predators in urban areas (Jokimäki and Huhta 2000). However, other studies suggest that urban habitats are "refuges" from predators, as both nests (Gering and Blair 1999; Ryder et al. 2010) and adult animals (McCleery et al. 2008) are predated less often in urban than in natural habitats. Some studies found no difference in nest mortality between habitats despite finding higher abundance of nest predators in more urbanized sites (Haskell et al. 2001). The apparent contradiction between the high abundance of nest predators and the lack of consistently higher nest mortality is referred to as the "urban predator paradox" (Rodewald et al. 2011a; Stracey 2011). Little is known about what causes this paradox.

Another method to investigate predation pressure is to observe the preys' antipredator behavior. A handful of studies used this approach, comparing vigilance (Coleman et al. 2008), mobbing behavior (Myers and Hyman 2016; Carrete and Tella 2017), or calming down after a simulated predator attack (Seress et al. 2011; Bókony et al. 2012a) between urban and non-urban animals. Generally, prey is expected to be more vigilant (and give stronger anti-predator responses) when predation risk is high, and less vigilant when predation risk is low. In urban habitats, predation risk may be influenced by a number of factors besides predator abundance.

For example, urban noise can mask a hunting predator; one study showed increased antipredator vigilance in traffic noise compared to ambient sound (Kern and Radford 2016). Non-anthropogenic food in urban habitats may also be scarce, and animals with limited access to food can afford less time and energy on antipredator behaviors (Duncan Rastogi et al. 2006).

The ubiquity of humans in cities may also affect the behavioral responses to predators. We may expect correlation between responses to humans and to non-human predators, for several reasons: (i) humans are likely to be perceived by most animals as a type of predator (Frid and Dill 2002; Beale and Monaghan 2004b), thus they may show a “general anti-predator response” towards both humans and non-humans; (ii) responses towards humans and non-human predators may both be part of a more general “boldness” behavioral syndrome (Myers and Hyman 2016; Carrete and Tella 2017); (iii) there may be a covariance between the abundance of humans and nonhuman predators, for example because predators have a stronger avoidance of humans than their prey (Møller 2012), a theory sometimes called “human shield” hypothesis (Geffroy et al. 2015); and (iv) environmental constraints like food availability can affect responses to both type of threats. As urban animals are generally less fearful from humans than their conspecifics in rural habitats (Samia et al. 2015), a potential correlation between responses to humans and non-human predators predicts weaker anti-predator responses in urban habitats. However, lower anti-predator vigilance could result in higher probability of getting predated, and thus higher mortality; this mechanism is called “human-mediated behavioral spillover” (Geffroy et al. 2015). One solution to avoid the negative consequences of the human-mediated behavioral spillover is to break down the potentially existing behavioral syndrome, and develop a tolerance specifically towards humans while remaining vigilant towards nonhuman predators (Myers and Hyman 2016; Carrete and Tella 2017). How responses to humans and to non-human predators relate to each other is still an open question.

CHAPTER 2

OBJECTIVES

During my doctoral studies, I explored how behavior towards humans and towards non-human predators changes with urbanization, by conducting behavioral experiments on two urbanized bird species, the house sparrow (*Passer domesticus*) and the great tit (*Parus major*) as part of the research projects of the Ornithology Research Group of the University of Pannonia (now called MTA-PE Evolutionary Ecology Research Group). Furthermore, I explored how nest predation changes along the urbanization gradient, by conducting a meta-analysis in collaboration with scientists from the Ludwig Maximilians University München, the Max Planck Institute for Ornithology, and the University of New South Wales.

Objective 1: Risk taking towards humans by urban and rural house sparrows

Tolerance towards humans is likely to be more advantageous for urban than for non-urban animals. This tolerance may be intrinsic or due to behavioral plasticity, e.g. habituation (see Introduction). In my first study (***Chapter 3***), I compared the fear responses of urban and rural house sparrows to humans, by measuring flight initiation distances in free-living flocks, and observing hiding behavior of wild-caught individuals in response to repeated human disturbance in captivity. I predicted that rural sparrows will be more fearful from humans in both situations. If the urban-rural difference in responses to humans is primarily intrinsic, then birds from the two habitats will significantly differ even at the first disturbance event in captivity, whereas in case of habituation, the responses will decrease over repeated disturbance faster in urban than in rural birds.

Objective 2: Discrimination between dangerous and non-dangerous humans

Differentiating between humans representing different levels of threat based on past experience can be advantageous in anthropogenic habitats, but little is known about whether animals from urban or from rural habitats are better at discriminating between people. In my second study (***Chapter 4***), I tested whether urban or rural house sparrows differ in this regard. Over a training period, the birds had the opportunity to learn to recognize a hostile and a non-hostile person. Following this, I tested whether urban and rural birds respond differently to these two persons as well as to a third, unfamiliar person, predicting that birds will differentiate between the three persons to a greater extent if they come from a habitat where encounters with humans are more frequent and/or recognizing humans is more advantageous.

Objective 3. Risk taking towards sparrowhawks and humans by urban and non-urban great tits

Responses to non-human predators can be affected by predation risk or other environmental factors, but may also be subject to a behavioral spillover effect due to being affected by the same physiological and cognitive mechanisms as responses to humans (see Introduction). In my third study (***Chapter 5***), I conducted behavioral experiments on great tits breeding in in urban and forest habitats. I first assessed similar questions to the previous two studies: do urban and forest birds respond differently to humans, and do they discriminate between an unfamiliar person and a familiar, hostile person to a different extent? Following this, I tested whether urban and rural great tits respond differently to a sparrowhawk (*Accipiter nisus*) mount, predicting that birds will be less fearful of it in a habitat where predation risk is lower and/or where there is an environmental or behavioral constraint. Finally, to explore the possibility of a spillover effect due to a behavioral syndrome, I tested whether the responses to the sparrowhawk are correlated with the responses to humans.

Objective 4. Urbanization’s effects on predation of bird nests: a meta-analysis

In my last study (***Chapter 6***), I carried out a systematic literature review and, using a formal meta-analytical approach, I tested whether predation on natural and artificial bird nests differs between urban and non-urban habitats. As differences between urban and rural habitats in the predator fauna and other environmental factors may both increase and reduce nest predation rate, I predicted that nest mortality will change (either increase or decrease) with urbanization. I also tested the possible confounding effects of study methods, study species and nest characteristics, as well as differences in definitions of predation rate or urbanization.

CHAPTER 3

RISK TAKING TOWARDS HUMANS BY URBAN AND RURAL HOUSE SPARROWS[1]

3.1. Introduction

In urban habitats animals are frequently exposed to the presence and various actions of humans. Due to their evolutionary background, wild animals often perceive humans as potential predators, and respond to their presence with flight (Blumstein 2014). However, anti-predator behaviors are costly because they take time and energy from other behaviors such as feeding and parental care that are important components of fitness (Lima 1998). Since people rarely pose real threat to urban wildlife such as birds (Clucas and Marzluff 2012), animals that live in urban habitats may benefit from decreasing their fear responses to humans. This idea is well supported by studies showing that animals in habitats with frequent human disturbance flee from humans at shorter distances (Metcalf et al. 2000; Møller 2008; McCleery 2009; Rodriguez-Prieto et al. 2009; Carrete and Tella 2011; Engelhardt and Weladji 2011; Keeley and Bechard 2011; Scales et al. 2011; Chapman et al. 2012; Clucas and Marzluff 2012; van Dongen et al. 2015; Cavalli et al. 2016).

Usually, the decreased fear response by urban animals is assumed to be a result of habituation to humans (Metcalf et al. 2000; McCleery 2009; Rodriguez-Prieto et al. 2009; Chapman et al. 2012). Habituation is defined as a reduced behavioral response to a repeated, neutral stimulus (Whittaker and Knight 1998; Blumstein 2014), therefore it is a form of behavioral plasticity and implies a learning process. However, two alternative mechanisms may also account for the reduced fearfulness of urban animals. First, if fearfulness varies greatly between but little within individuals, the less fearful individuals are expected to move to and settle in cities more often than the more fearful individuals; this theory is referred to as differential colonization hypothesis (Møller 2010a), or sometimes habitat selection hypothesis (Carrete and Tella 2010) or differential recruitment hypothesis (Blumstein 2014). For example, a study of flight initiation distances (FID; a frequently used proxy for wild animals' fear from humans) found that species with the highest inter-individual variance in FID at their original,

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[1] This chapter is a modified version of the research article „Ernő Vincze, Sándor Papp, Bálint Preiszner, Gábor Seress, Veronika Bókony & András Liker (2016): Habituation to human disturbance is faster in urban than rural house sparrows. Behavioral Ecology 27: 1304-1313".

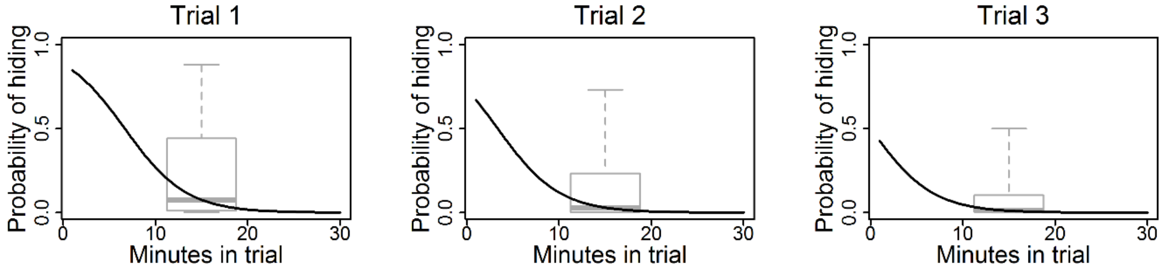
rural habitats are the most successful in colonizing cities (Carrete and Tella 2011). Second, bold urban phenotypes may also result from selection in urban habitats that allows individuals with low intrinsic fearfulness to realize high fitness; this theory is known as local adaptation hypothesis (Møller 2008). In contrast to habituation, which involves behavioral plasticity, both the differential colonization and local adaptation hypotheses assume that fearfulness from humans varies consistently among individuals, a core concept of animal personality (Dingemanse et al. 2010). Such individual consistency in tolerance of human proximity has been found in several species (Carrete and Tella 2010; Evans et al. 2010; Scales et al. 2011; Végvári et al. 2011). Some studies suggest genetic differences underlying fear behaviors between urban and rural populations, which supports the differential colonization and/or local adaptation hypotheses (Mueller et al. 2013; van Dongen et al. 2015).

The above three mechanisms are non-exclusive, and there may also be selection for individuals with higher behavioral plasticity and better habituation ability, instead of a certain behavioral type (Dingemanse et al. 2010). Very few studies have specifically investigated whether individuals of wild animals differ in their rate of habituation to human disturbance, but they all found significant inter-individual variation (Runyan and Blumstein 2004; Ellenberg et al. 2009; Carrete and Tella 2010). Such variation may be the basis of selection for better habituation abilities in urban habitats, but whether urban individuals indeed habituate faster to human disturbance than their rural conspecifics has not yet been demonstrated. Furthermore, habituation may come about in any, but not necessarily every parameter of a certain behavior (Rankin et al. 2009); for example, by decreasing reactivity (i.e. the initial response to a specific disturbance event) or by speeding up recovery (i.e. the time during which the response persists after the disturbance has ended) over the course of repeated disturbance events (Figure 3.1). These two aspects of coping with disturbance do not necessarily covary (Linden et al. 1997).

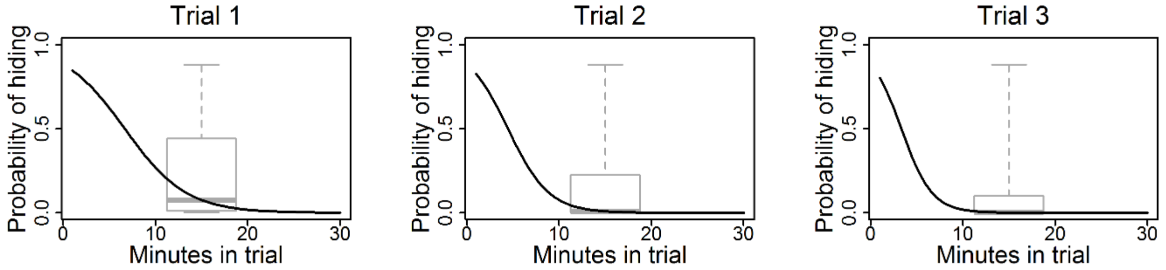
In this study our aim was to examine whether fearfulness from humans and the rate of habituation to human disturbance differ between urban and rural individuals in the house sparrow (*Passer domesticus*). After quantifying the sparrows' fear response to humans in the field, we placed both urban and rural birds in an unfamiliar situation and observed their habituation to repeated human disturbance by looking at the changes in their reactivity, recovery, and overall fearfulness (which encompasses both reactivity and recovery). We predicted that if differential colonization or local adaptation for bolder behavior are mainly responsible for the reduced fearfulness of urban birds, then they should show less fear from humans (i.e. lower reactivity and/or faster recovery following the disturbance events) than rural birds, even at the first encounter with the novel disturbance. We expected faster habituation (i.e.

faster change across trials in their reactivity and/or recovery, Figure 3.1) by urban than by rural birds if this type of behavioral plasticity plays an important role in the bolder behavior in urban habitats.

(a) Habituation by reactivity



(b) Habituation by recovery



(c) Habituation by reactivity & recovery

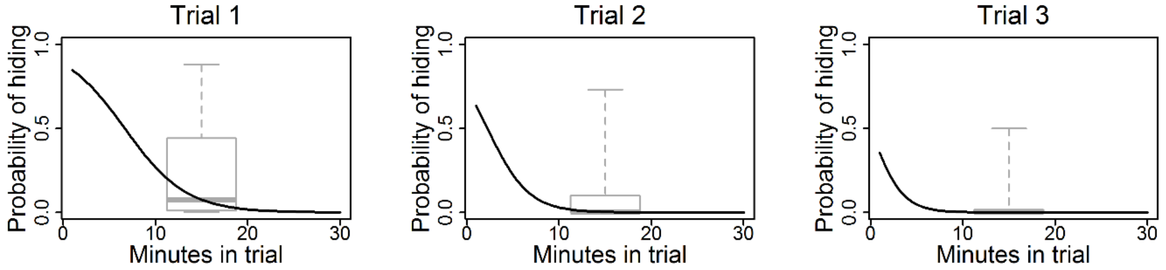


Figure 3.1: *Illustration of 3 hypothetical cases of habituation over 3 disturbance trials. For each trial, the boxplot shows the among-individual variation in the proportion of records in which the bird was hiding ("hiding frequency") during the trial. The black curves show the average response of the birds in each trial (among-individual variation would be represented by several different curves on the same graph; these are omitted for clarity). For each curve, the intercept expresses the probability at which the birds were hiding at the beginning of the trial ("reactivity"), whereas the slope expresses the speed of decrease in the probability of hiding within the trial ("recovery"). We refer to hiding behavior in the first trial as "intrinsic boldness", and to the across-trial change of behavior as "habituation". The latter can occur by decreasing (a) reactivity, (b) recovery or (c) both across the trials; all resulting in reduced hiding frequency.*

Figure 3.2: *Male house sparrow in an urban habitat. Photograph by Bálint Preiszner.*

3.2.Methods

3.2.1. Study species

The house sparrow (Figure 3.2) is a small (23.1-34.9 g, Bókony et al. 2012b) granivorous bird from the order Passeriformes and the family Passeridae (Summers-Smith 2009). It has a long evolutionary history with humans, having lived exclusively in anthropogenic habitats, from farmlands to city centers, since ancient times (Shaw et al. 2008; Summers-Smith 2009; Sætre et al. 2012). In winter it shows gregarious behavior, with flocks that range from a handful to hundreds of individuals (see Table A3.1 for examples of flock sizes). Adult house sparrows show sexual dimorphism in plumage coloration, which makes sexing the birds very easy (Summers-Smith 2009).

Thanks to their long history of commensalism with humans and easy accessibility, house sparrows are excellent subjects of behavioral ecology studies (Anderson 2006). Our research group has studied house sparrows for over a decade, investigating differences between urban and rural populations. These studies revealed that sparrows are significantly larger in rural than in urban habitats (Liker et al. 2008), although their overall body condition is similar in the two habitat types (Bókony et al. 2012b). This difference is likely to be explained by differences in nestling diet (Seress et al. 2012). Furthermore, although there is a great variation in their competitive performance, it does not differ between urban and rural populations (Bókony et al. 2010). However, flock size and urbanization both have positive effect on problem solving abilities (Liker and Bókony 2009). Furthermore, there is no consistent difference between urban and rural sparrows in fear from novel objects and predators (Bókony et al. 2012a); the latter shows an age-dependent effect, with young urban birds being less fearful and old urban birds being more fearful of a sparrowhawk than rural birds (Seress et al. 2011).

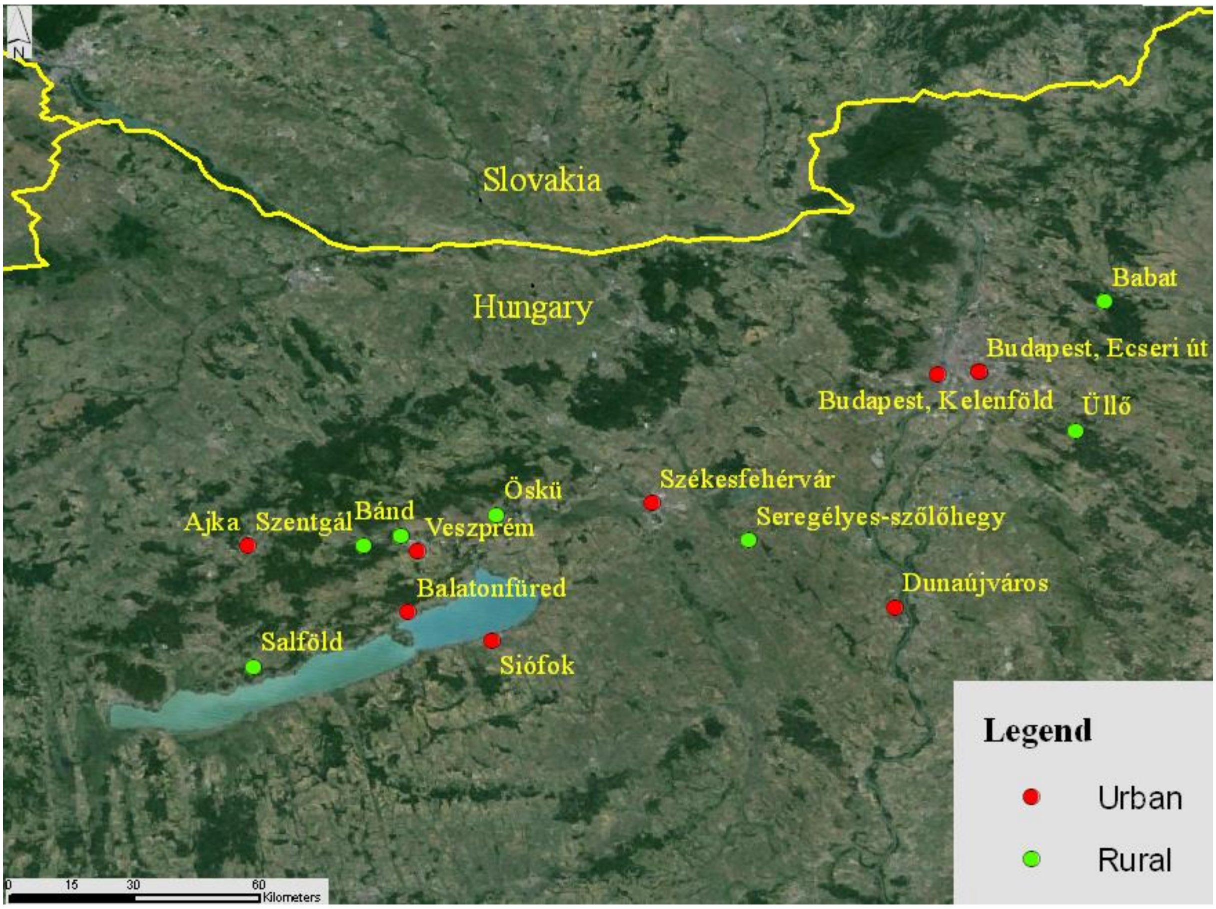


Figure 3.3: *Geographical location of the study sites. Image created by Tamás Hammer in ArcGIS.*

3.2.2. Study sites

We studied house sparrows in 15 differently urbanized habitats in Hungary (Figure 3.3, Table A3.1). We focused on sites from the two extremes of the urbanization gradient occupied by the species, that is, remote farms or edges of small villages, and densely built inner city centers. To verify our choice of sites, we quantified the urbanization of the capture sites based on 4 habitat features: building density, vegetation cover, presence of roads, and human population density. First, we scored the digital aerial photograph of each site using the *UrbanizationScore* image-analysis software (Seress et al. 2014) based on the methods of Liker et al. (2008). A 1-km^2 area around the site of capture was divided into 10 × 10 cells, and each cell was assigned a score for vegetation cover (0: absent, 1: <50%, 2: >50%), density of buildings (0: absent, 1: <50%, 2: >50%), and presence of paved roads (0: absent, 1: present).

From these cell scores we calculated 5 habitat characteristics for each site (mean vegetation density, mean building density, number of cells with roads, and number of cells with >50% vegetation and buildings, respectively). Then, following Bókony et al. (2010) we collected data on the density of residential human population for each settlement from the Hungarian Central Statistical Office; for the 2 sites in Budapest, we used the data for the respective districts of the capital. For 3 farm sites we ascertained population density by either asking the residents (family farm at Szentgál) or consulting the website of the farms (Üllő-Dóramajor and Babat). Then we included the above 5 habitat characteristics and $\log_{10}$-transformed human population density in a principal component analysis, which resulted in a single axis with >1 eigenvalue that explained 93.4% of total variance, and correlated strongly negatively with mean vegetation density ($r = -0.98$) and number of cells with high vegetation density ($r = -0.99$), and strongly positively with mean building density ($r = 0.99$), number of cells with high building density ($r = 0.97$), number of cells with roads ($r = 0.99$), and human population density ($r = 0.88$). We refer to the scores along this axis as “urbanization score”.

Based on these scores, we divided the capture sites into 2 groups (henceforth “urbanization category”): “urban” (positive urbanization score) and “rural” (negative urbanization score). These categories matched our initial, subjective categorization of urban and rural sites in all cases (see Table A3.1 for further details). This categorization also clearly separated sites with high and low human population density (182–4315.5 residents / km^2 for urban sites, 3.6–64.9 residents / km^2 for rural sites). We used the urbanization categories in the analyses because this approach involves fewer statistical assumptions (i.e. it is not known if human population density and/or landscape composition adequately reflect the fine-scale between-site variation in those conditions that are most relevant for house sparrows’ fearfulness). Nevertheless, we repeated all analyses by replacing urbanization category with urbanization score, and our results were qualitatively unchanged.

3.2.3. *Flight initiation distance in the field*

FIDs were measured by a single observer (Sándor Papp) at each of the 15 sites (Table A3.1) between December 2011 and March 2012. Whenever the observer spotted either a single house sparrow or a flock while searching for them along random transects, he walked towards them in a straight line at a constant speed with constant pace length (repeatedly measured as 0.75 m). The observer noted his starting distance (mean ± *SD* = 11.72 ± 8.17 m), as it may significantly affect the FID (Blumstein 2003; Rodriguez-Prieto et al. 2009; Atwell et al. 2012). Since sparrows are gregarious and seldom feed alone, we included both flocks and single individuals.

The distances at which the first and the last individual of a flock fled, respectively, were recorded in all cases (since in 46% of the flocks, the birds did not take off at the same time) by counting the number of paces. For an overview of how FID was measured, see Figure 3.4.

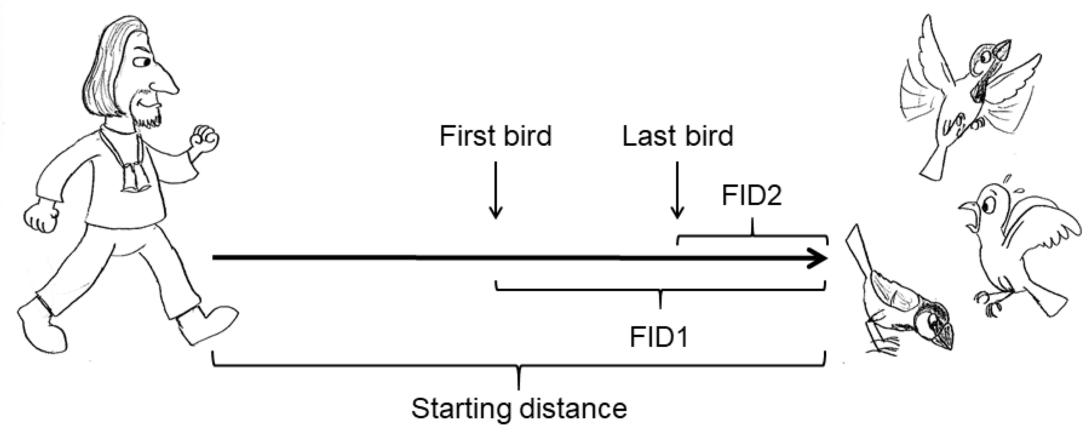


Figure 3.4: *Schematic of the test protocol of the flight initiation distance measurements. Sketches by the author.*

We also recorded the following variables that may influence the birds' perception of threat: time of day, flock size (the estimated number of sparrows in the flock), presence or absence of other bird species in the flock, and flock position (i.e. whether the birds were on the ground or perching on a bush or a fence). We included off-ground FIDs because sparrows were more often found perching instead of on the ground (88.4% in our FID records); note however that the proportion of ground and off-ground FIDs was very similar at our urban and rural sites (89.2% and 87.4%; χ^2 test: $\chi^2_1 = 0.10$, $P = 0.748$). FID is often measured off-ground in species that spend a considerable amount of time perching (Metcalf et al. 2000; Blumstein 2003; Valcarcel and Fernández-Juricic 2009; Scales et al. 2011), and perching birds do not always have a shorter FID than those on the ground (Blumstein et al. 2004).

Since the birds were unmarked, different flocks measured at the same site may contain the same individuals; to reduce the potential for pseudo-replication the observer walked for at least 15 minutes between consecutive measures. Note that wintering flocks of sparrows normally have home ranges of several hundred meters (Liker et al. 2009). A moderate degree of pseudo-replication did not qualitatively affect the results of analyses examining the relationship between FID and other variables in another study (Runyan and Blumstein 2004). Observations where the flock got startled from another source of disturbance (such as another human, a dog or a car) instead of the observer were excluded from the analysis. At each site, we took 8 to 16 (mean ± $SD = 10.9 \pm 2.4$) measures over the course of up to 9 days (mean ± $SD = 3.9 \pm 2.0$

days), with up to 10 measures per day (mean ± *SD* = 2.8 ± 1.8), resulting in FID records from 156 flocks' first and last individuals and 7 single birds that were treated as first individuals (Table A3.1).

3.2.4. Habituation in captivity

We captured house sparrows with mist nets between January and March 2012 from the same sites where we measured FID. Over 8 weeks, we captured sparrows each week from 2 sites of the same urbanization category, alternating urban and rural sites weekly. We henceforth will refer to a weekly group of birds as "cohort". Each cohort consisted of 10 to 14 birds, resulting in a total sample size of 97. At capture, we measured each bird's tarsus length (± 0.1 mm), and ringed them with an individually numbered metal ring. Then the birds were transported to Veszprém and housed indoors, where they participated in a series of studies as part of a more general project (Bókony et al. 2014; Papp et al. 2015; Preiszner et al. 2015).

Each cohort was captured over 2 days (days 1-2) and spent the following 3 days in individual cages while participating in a behavioral experiment (Papp et al. 2015), during which they were exposed to little disturbance, i.e. they were briefly approached by a human only twice per day, in contrast with the 12 daily approaches of the habituation regime (see below). On day 5 in the afternoon, we weighed the birds (± 0.1 g) and moved them into a new room used for the present study where they were allowed to acclimate for 2 days (days 6-7). Then the birds were observed in 8 trials involving human disturbance over 2 days (days 8-9) as described below. As the birds were completely undisturbed by humans during the days of acclimation, we considered the first trial as a novel situation where they first experienced human approach in the new housing room. After the present study, the birds participated in further experiments, and then, they were released as detailed elsewhere (Preiszner et al. 2015).

The birds were housed individually in 42×30×35 cm cages, each containing 2 perches and a vertical plastic sheet hanging from the top of the cage as shelter. All 14 cages were in the same room, positioned on 3 shelves and visually separated from each other with opaque plastic boards (Figure 3.5). About 2.5 meters away from the cages there was a curtain behind which the experimenter could hide. During the study, water was provided *ad libitum*, amended by multivitamin droplets. Food (millet seeds) was constantly available to 26 birds (14 urban and 12 rural) in a transparent plastic dish (7.5-cm diameter, 3.5-cm high), whereas 71 birds (35 urban and 36 rural) were fasted for an hour before each trial as part of another study (Preiszner et al. 2015). The latter birds received their food in a white plastic box (8.5 × 8.5 × 2.5 cm) with a lid on the top which had to be opened up to access the seeds; this feeding method was unfamiliar for all 71 birds in the first trial, but 73% of them (52 birds) learned to use it by the end of the 8th trial (Papp et al. 2015). Between-individual variation in food availability and within-individual variation in feeder-opening success were taken into account as confounding variables in the statistical analyses.

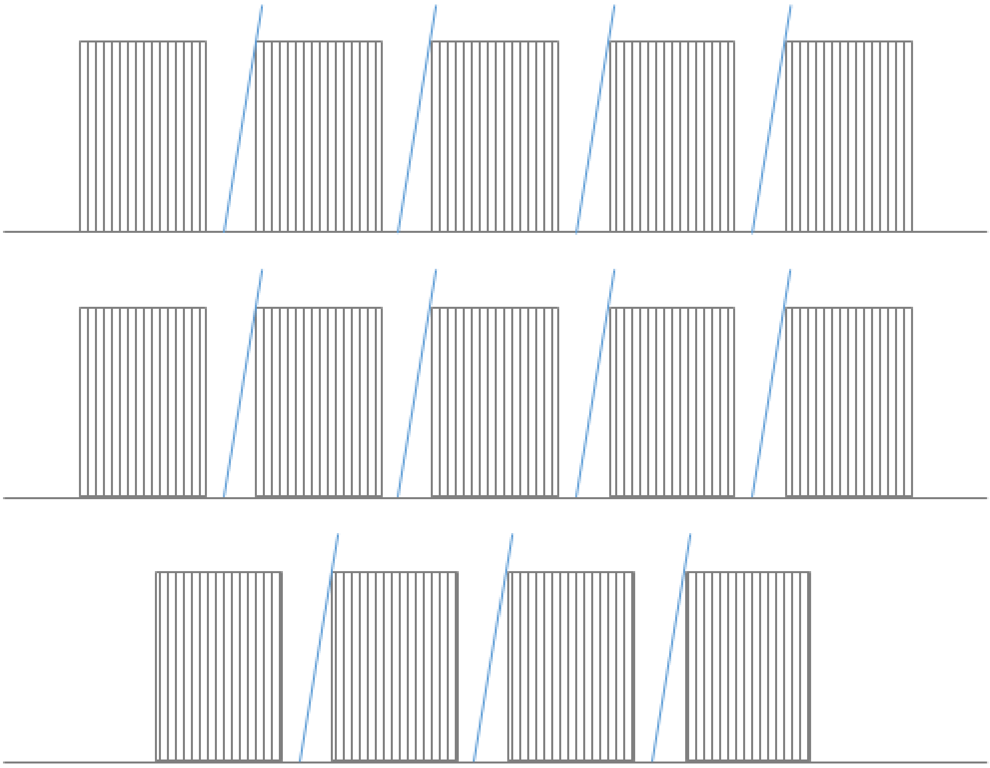


Figure 3.5. *Schematic of the placement of the 14 cages in which a cohort of sparrows was housed*

On days 8-9, the birds were observed in 4 trials each day as follows. Each trial started after a 60-minute resting period (during which the birds with the openable feeder were fasted), consisted of a circa 5-minute disturbance phase and a 30-minute observation period, and was followed by a 15-minute feeding period. During the disturbance phase, I approached the cages in randomized order, and disturbed each bird by placing an openable feeder in the cage of the fasted birds and replacing the feeder dish of the non-fasted birds with an identical dish. Then I hid behind the curtain and observed the birds simultaneously through a one-way window. I scanned the birds every 3 minutes (thus observing each bird for ca. 15 seconds within a 3-minute time window), and recorded their behavior for each time window as one or more of the following categories: hiding behind the shelter, resting non-hidden in the cage, hopping, flapping, perching on or next to the feeder, attempting to feed (i.e. manipulating the feeder with the beak), feeding, drinking, preening, engaging in stereotypical movements such as biting on the cage bars or pushing head through the bars (this occurred in only 3% of records). Thereby

10 records of each bird's behavior were collected in each trial. We only analyzed hiding behavior in this study; the other behavioral categories were collected for other studies (Bókony et al. 2014; Papp et al. 2015). After 30 minutes of observation, I fixed the feeder lids in open position in all of the cages, and then left the birds undisturbed for 15 minutes so that all of them could feed. Finally, following this feeding period, the openable feeders were removed from the cages while the dishes were replaced in randomized order, as above, and the next 60-minute resting period started. The 4 trials were distributed evenly within each day between 8:00 and 16:00; lights were on from 7:00 till 17:00, allowing the birds to feed freely for 1 hour each before the first fasting and after the last trial. Although this general protocol was continued on days 10-12, here we analyzed the data from days 8-9 only, because some aspects of the protocol varied among birds in the last 3 days as part of another study (Preiszner et al. 2015).

3.2.5. Statistical analyses

To see if FID varied consistently among study sites, we calculated the site-specific repeatability of FID following Lessells and Boag (1987). The effects of urbanization and other factors on FID were analyzed with a linear mixed-effects model that allowed the response variable to have different variance in urban and rural habitats. We included the following explanatory variables in the initial model: urbanization category, starting distance, flock size, flock position (ground or perching), date (expressed as the number of days since the 1st of December, 2011), time of day (expressed as the number of minutes since 6:00 AM), presence of other species, flight order (i.e. if the FID was of the first or the last individual's in the flock), and the interaction between urbanization category and flight order (to test whether the habitat effect depends on the type of measurement, i.e. first or last fleeing flock-members). We included study site and flock ID as nested random factors (i.e. the first and last individuals of the same flock were treated as repeated measures).

In the captive birds, to quantify fearfulness and its decrease over time (i.e. habituation), we focused on hiding behavior, since sparrows often responded to the approach of the experimenter by hiding behind the shelter in their cages. While hiding behavior in captivity is not the exact equivalent of FID in the wild, both forms of behavior are related to avoidance of humans and therefore may possibly be influenced by similar underlying mechanisms. For each bird in each trial, we estimated the proportion of time spent in shelter (henceforth "hiding frequency") as the proportion of records (out of all 10 records per trial) when the bird was observed hiding behind the shelter. Because sometimes both hiding and one or more other behaviors were observed in the same record (e.g. if the bird was coming out from behind the shelter and started to engage in another activity, then both behaviors were recorded), hiding frequency was corrected for the total number of behaviors observed in the 10 records (e.g. if a bird was seen hiding in 1 out of 10 records, then it got a hiding frequency score of 0.1 if it was observed fully hiding within the record, but 0.05 if it was coming out of the shelter and engaging in another behavior).

First, we compared urban and rural birds' fearfulness in the first trial as a proxy for intrinsic boldness. We used hiding frequency as response variable in a generalized linear mixed-effects model with quasi-binomial error distribution and logit link function, and cohort ID as random factor to control for the non-independence of birds tested together (i.e. in the same week). We did not use the capture site as a random factor in this model, as it was neither independent from cohort (most sites were used in only one cohort) nor completely nested in it (one site was used in two separate cohorts). Therefore, the two factors did not meet the conditions of either a crossed or a nested random factor structure (Schielzeth and Nakagawa 2013). We included the following explanatory variables in the initial model: urbanization category, vertical and horizontal position of the cage, sex, food treatment (fasted or not), and body condition calculated as the scaled mass index proposed by Peig & Green (2009) using the equation: body mass × $(19/\text{tarsus length})^{1.71}$ (Bókony et al. 2012b).

Then we investigated the rate of habituation in two sets of analyses. The first analysis used the same modelling framework as the analysis of hiding frequency in the first trial, but here we used the data of all 8 trials, and added trial number and its interaction with urbanization as explanatory variables. To be able to express the rate of habituation as the decrease of hiding time over consecutive trials, we used trial number as a continuous variable (thus assuming a linear change over time). The initial model included cohort ID and bird ID as nested random factors, and the same potentially confounding variables as listed above. In addition, we controlled for variation in access to food, i.e. whether or not in each trial the individual could access the food in its feeder ("yes" for non-fasted birds and for those fasted birds that had learnt to open the feeder in previous trials, "no" for fasted birds that had not yet used the feeder before), by including it as an additional term in our models.

To examine the change of hiding behavior in more detail, we conducted a second set of analyses in which we considered changes not only across trials but also within trials, to separately investigate the two aspects of habituation: reactivity, i.e. the immediate response to disturbance at the beginning of a trial, and recovery, i.e. the rate of calming down after the disturbance within a trial (Figure 3.1). To do so, we modelled the temporal change in the occurrence of hiding over the 30-minute trial for each bird. First, for each of the 8 trials we built a generalized linear mixed-effects model with quasibinomial error and random intercepts and random slopes for each individual, with the occurrence of hiding (i.e. whether hiding behavior occurred or not in each scan sample, either by itself or together with other behaviors) as the response variable and time of sampling (i.e. order of the 3-minute records) within trial as the explanatory variable. From these models we extracted, for each individual in each trial, the intercept and slope estimates. Then we used the intercepts as an estimate of the birds' reactivity to human disturbance (i.e. the probability of hiding at the start of the trial). The slopes, on the other hand, provide an estimate of the speed by which the fear response decreased within the trial, i.e. the rate of recovery. However, the slopes are not independent from the intercepts because the individuals that were less fearful at the start had less steep slopes (Spearman rank correlation: $R_s = -0.73$, $P < 0.001$). Therefore we estimated the recovery rates by calculating the residuals of a standardized major axis regression that included the slope estimates of the previous model as response variable and the intercept estimates as the explanatory variable. Thus, these residuals express how fast the individual recovered relative to how strongly it reacted initially; larger negative values mean faster recovery rate. Then we analyzed how reactivity and recovery rate changed across the trials in urban and rural birds in 2 respective linear mixed-effect models that included trial number as a continuous variable, and its interaction with urbanization category. Both initial models included vertical and horizontal position of the cage, sex, food treatment, access to food, and body condition as potentially confounding variables, and cohort ID and bird ID as nested random factors.

In each analysis, we removed non-significant terms stepwise until only $P < 0.05$ terms remained, except that we never omitted urbanization because this was the effect we aimed to test specifically. In the analyses of habituation rates, we always retained trial number because it was necessary for quantifying the rates of habituation. In the analysis of FID, we retained the interaction between flight order and urbanization, and used linear contrasts with correction for false discovery rate (Benjamini et al. 2001) to test if habitat difference is present in both the first and last fleeing individuals of the flocks. We also present our full initial models, with both significant and non-significant terms, in Table A3.2, and the model diagnostic plots of our final models in Figure A3.1. All analyses were run in R 3.0.2, using the 'nlme' and 'multcomp' packages.

3.3.Results

3.3.1. Flight initiation distance in the field

FID varied consistently among the study sites, as shown by its high repeatability ($R = 0.795$, $F_{14,304} = 41.6$, $P < 0.001$). On average, FID was about 4 meters longer at rural sites than at urban sites (Table 3.1, Figure 3.6). The difference between urban and rural FIDs was slightly larger in the first-fleeing individuals than in the last-fleeing individuals (Table 3.1, Figure 3.6), but post-hoc tests revealed that the habitat difference was highly significant among the first and last birds alike (linear contrasts, urban-rural difference in the first-fleeing birds: -4.44 ± 0.92 m, in the last-fleeing birds: -3.75 ± 0.92 m, both $P < 0.001$). Birds on the ground and in larger flocks fled from greater distances than perching birds and those in smaller flocks; FID also increased with starting distance and decreased with calendar date (Table 3.1).

Table 3.1: *Flight initiation distance in wild house sparrows in relation to habitat type, flight order (first or last fleeing), and other variables. Parameter estimates (b) of the final linear mixed-effects model are shown.*

Fixed effects	***b***	**± *SE***	***df***	***t***	***P***
Intercept (urban, last fleeing, ground) [a]	1.155	± 1.234	154	0.936	0.358
Habitat (rural vs. urban) [b]	3.750	± 0.918	13	4.086	0.001
Flight order (first vs. last) [b]	0.680	± 0.138	154	4.917	<0.001
Habitat × Flight order [c]	0.691	± 0.367	154	1.884	0.062
Starting distance [d]	0.433	± 0.044	144	9.807	<0.001
Flock size [d]	0.099	± 0.031	144	3.183	0.002
Position (perching vs. ground) [b]	-2.894	± 0.760	144	-3.809	<0.001
Date [d]	-0.032	± 0.013	144	-2.436	0.016
Random effects	***SD***				
Site	1.451				
Group ID in Site	2.426				
Residual variance	0.903				

[a] *In this and the following tables, the parameter estimate (b) for the intercept shows the average value of the dependent variable in the reference category, which is defined in brackets following "Intercept".*

[b] *For categorical variables (fixed factors), b for each category shows the difference (in the average value of the dependent variable) of that category from the intercept (e.g. perching flocks had 2.89 m shorter FIDs than flocks on the ground). If the factor is in interaction with another factor, the parameter estimate refers to the difference between the categories of this factor while the other factor is at the intercept value (e.g. rural FIDs were 3.75 m longer than urban FIDs in the case of last-fleeing flock members).*

[c] *Interaction terms express how the difference between 2 categories of one factor differs between 2 categories of another factor (e.g. the difference between first and last fleeing flock-members, which is 0.68 m in urban birds, is by 0.691 m larger in rural birds; similarly, the difference between urban and rural birds is by 0.691 m larger in the first-fleeing birds than in last-fleeing birds).*

[d] *For numeric predictors, b shows the slope of the regression line (e.g. if the starting distance increases by 1 m, FID increases by 0.433 m on average).*

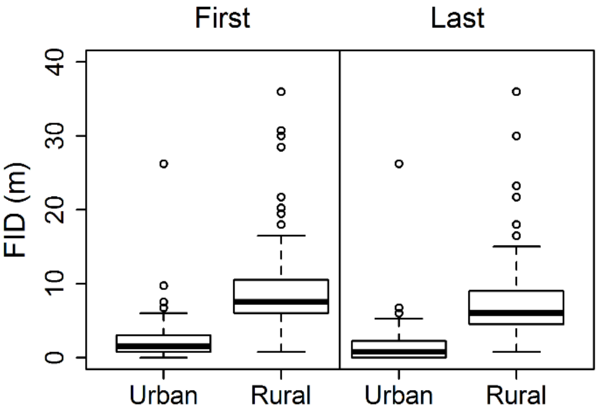


Figure 3.6: *Flight initiation distances of the first and last fleeing members of house sparrows flocks at urban and rural sites. Boxplots show the median and the upper and lower quartiles, with the whiskers representing data within the 1.5 × inter-quartile range.*

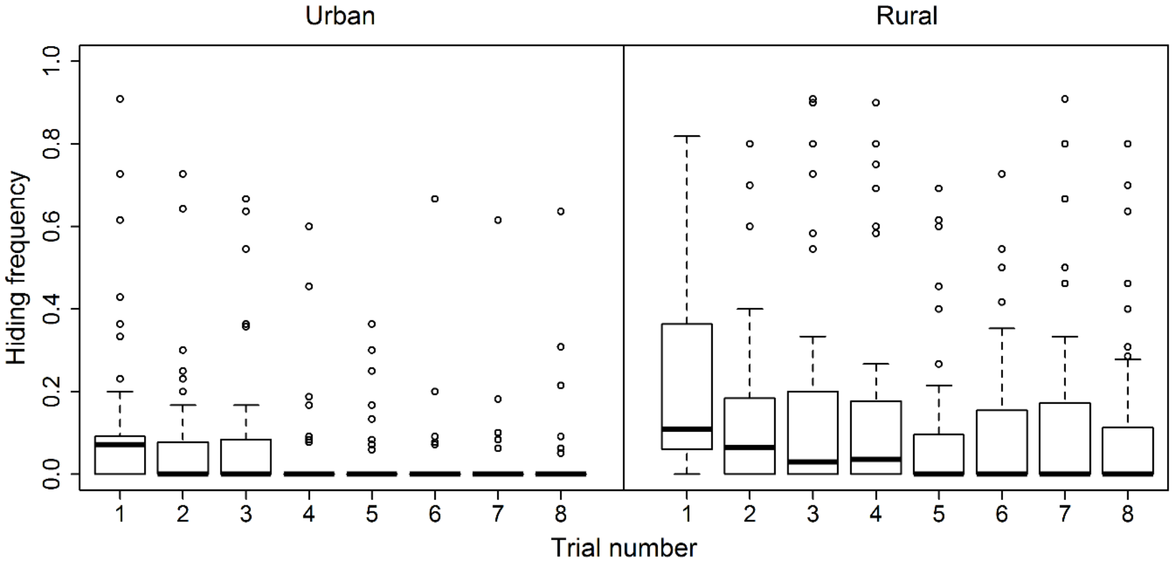


Figure 3.7: *Hiding frequency of urban and rural birds in the 8 trials (see Figure 3.6 for the interpretation of boxplots).*

3.3.2. Habituation in captivity

In the first trial, hiding frequency did not differ significantly between urban and rural birds (Table 3.2A, Figure 3.7). Over the 8 trials, hiding frequency decreased significantly, and the rate of this decrease was faster in urban than rural birds (Table 3.2B, Figure 3.7). Within trials, the occurrence of hiding was highest at the start of the trial and then decreased over the 30 minutes (Figure 3.8). Reactivity decreased across trials, meaning that the birds were less likely to hide at the start of later trials than at the start of earlier trials (Table 3.2C, Figure 3.8). In the very first trial, the proportion of individuals that were hiding in the first 3 minutes did not differ significantly between urban (55.1%) and rural birds (70.8%; χ^2 test: $\chi^2_1 = 1.94$, P = 0.164; see also Table 3.2C). However, we found a significant interaction between habitat type and trial number, i.e. the decrease in reactivity across trials was less steep in rural birds (Table 3.2C, Figure 3.8). Recovery rate also showed a trend of getting faster (i.e. larger negative slope values) after the first trial (Table 3.2D, Figure 3.8), however, there was no significant interaction between habitat type and trial number (P = 0.916), i.e. urban and rural birds showed similar change in recovery rate across trials. Furthermore, the difference between urban and rural birds' recovery rates was not significant (Table 3.2D).

Table 3.2: *Test statistics with parameter estimates (b) of the final generalized linear mixed-effect models on the behavior of captive house sparrows in relation to habitat type. Higher values mean that the bird spent more time hiding during the trial (A, B) or was more likely to hide at the beginning of the trial (C), whereas in table D, lower (i.e. more negative) values mean that the bird's recovery was more rapid (i.e. probability of hiding decreased faster) within the trial. In models A and B, the error distribution of the model was quasi-binomial; the interpretation of parameter estimates (as described in the footnotes of Table 3.1) applies to the logit-transformed values of the dependent variable in these 2 models.*

A) Hiding frequency in the first trial					
Fixed effects	***b***	**± *SE***	***df***	***t***	***P***
Intercept (urban, top shelf)	-2.486	± 0.600	87	-4.141	<0.001
Habitat (rural vs. urban)	0.965	± 0.777	6	1.242	0.261
Position (middle shelf vs. top shelf)	-0.025	± 0.337	87	-0.074	0.942
Position (bottom shelf vs. top shelf)	0.696	± 0.325	87	2.145	0.035
Random effects	***SD***				
Cohort ID	0.986				
Residual variance	0.449				
B) Change in hiding frequency over 8 trials					
Fixed effects	***b***	**± *SE***	***df***	***t***	***P***
Intercept (urban, top shelf, first trial)	-2.605	± 0.489	677	-5.327	<0.001
Trial number	-0.333	± 0.040	677	-8.270	<0.001
Habitat (rural vs. urban)	0.488	± 0.608	6	0.804	0.452
Trial number × habitat	0.171	± 0.048	677	3.569	<0.001
Position (middle shelf vs. top shelf)	-0.169	± 0.376	87	-0.451	0.653
Position (bottom shelf vs. top shelf)	1.044	± 0.383	87	2.724	0.008
Random effects	***SD***				
Cohort ID	0.699				
Bird ID in Cohort ID	1.318				
Residual variance	0.327				

C) Change in reactivity to human disturbance over 8 trials					
Fixed effects	***b***	**± *SE***	***df***	***t***	***P***
Intercept (urban, not fasted, can access food, first trial)	2.458	± 0.825	676	2.980	0.003
Trial number	-1.314	± 0.080	676	-16.452	<0.001
Habitat (rural vs. urban)	0.825	± 1.044	6	0.791	0.459
Trial number × habitat	0.249	± 0.107	676	2.325	0.020
Treatment group (fasted vs. not fasted)	-1.417	± 0.549	88	-2.578	0.012
Access to food (no vs. yes)	1.015	± 0.408	676	2.488	0.013
Random effects	***SD***				
Cohort ID	1.151				
Bird ID in Cohort ID	1.788				
Residual variance	3.418				
D) Change in recovery rate over 8 trials					
Fixed effects	***b***	**± *SE***	***df***	***t***	***P***
Intercept (urban, top shelf, first trial)	-0.455	± 0.044	678	-10.451	<0.001
Trial number	-0.004	± 0.002	678	-1.772	0.077
Habitat (rural vs. urban)	0.089	± 0.053	6	1.652	0.150
Position (middle shelf vs. top shelf)	-0.006	± 0.033	87	-0.180	0.857
Position (bottom shelf vs. top shelf)	0.100	± 0.035	87	2.892	0.005
Random effects	***SD***				
Cohort ID	0.065				
Bird ID in Cohort ID	0.124				
Residual variance	0.150				

Birds on the bottom shelf spent more time hiding and had less steep recovery rates than those on the top and middle shelves (Tables 3.2A, B and D); vertical cage position had no significant effect on reactivity. Food treatment and access to food had significant effects on reactivity: birds that were fasted before the test, and those that knew how to open the feeder, were less likely to hide in the beginning of the trial than either non-fasted birds or those that were unable to access their food (Table 3.2C). Horizontal cage position, sex, and body condition did not have significant effect on any response variable and were omitted from the final models.

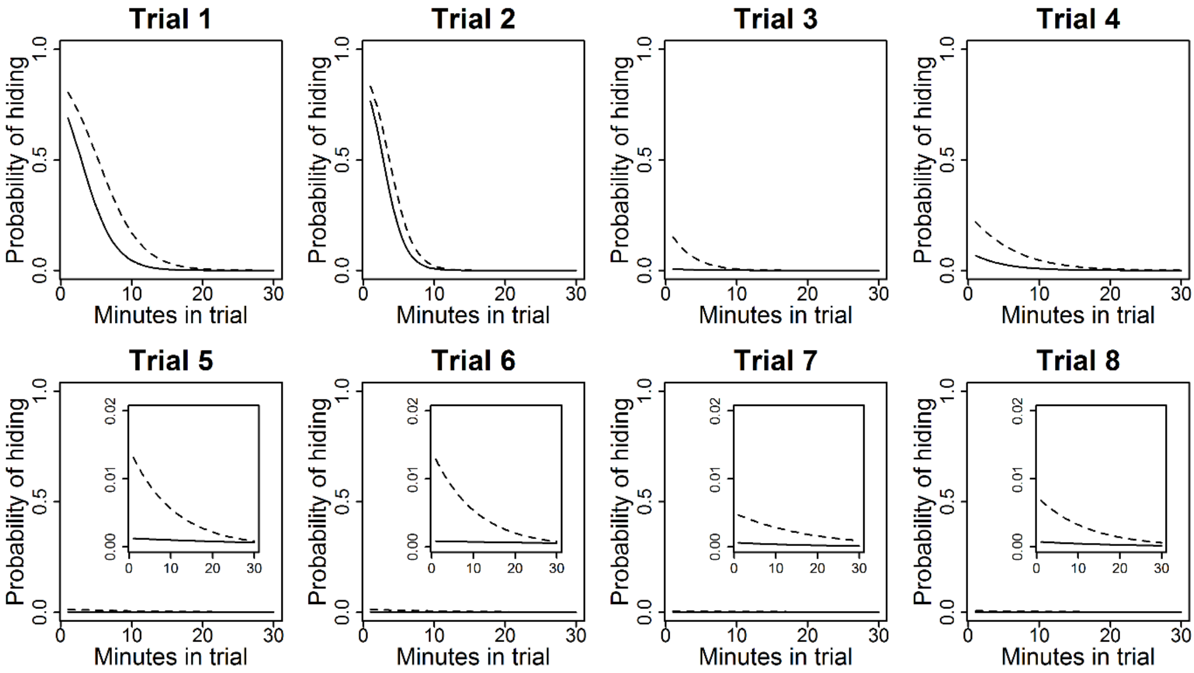


Figure 3.8: *Changes in the probability of hiding over 30 minutes after human disturbance for urban (solid line) and rural (dashed line) birds within each trial, as predicted from the models in Tables 3.2 C and D. The inlet plots for trials 5 to 8 show the data with the range of the Y axis set to 0-0.02, to help within-trial comparison of urban and rural birds.*

3.4. Discussion

Our results show that, despite urban house sparrows showing much shorter FIDs in the field than rural conspecifics, birds of both habitat type responded similarly to human disturbance in captivity when they encountered the test situation for the first time. While individuals from both habitat types showed habituation during repeated exposure to the same disturbance, urban individuals habituated significantly faster than rural individuals, and they did so by decreasing their immediate response (reactivity) to the disturbance. Although the few days of pre-test captivity may have influenced the behavior of birds, this is not likely to explain the similarity of the birds' initial response because faster habituation by urban individuals should intensify, not reduce, any pre-existing fear differences. Taken together, these results support the hypothesis that habituation to humans can play a significant role in the tameness of urban animals.

The shorter FID we found in urban house sparrow populations compared to rural ones is in line with what several other studies found, i.e. individuals from habitats with higher human disturbance flee from closer distances than those from less disturbed habitats in most species (Blumstein 2014), including house sparrows (Clucas and Marzluff 2012). Both the first and last fleeing members of the house sparrow flocks in our study showed a significant difference between urban and rural habitats. Other studies that measured the FID of a random individual of the flock (Carrete and Tella 2011) or the closest individual to the observer (Rodriguez-Prieto et al. 2009) also found shorter FIDs in habitats with more human disturbance, which suggests that this effect is robust regardless of the method of selecting focal individuals. However, when birds from the same populations in which we found FID differences were subjected to a novel kind of human disturbance in captivity, we found no strong difference between urban and rural birds in their initial fear responses. The same lack of difference was also reported by other studies that compared the behavior of urban and rural birds under standardized captive conditions; for example, in the "control tests" of personality assays where the birds were exposed to brief human disturbance, neither house sparrows (Bókony et al. 2012) nor blackbirds (*Turdus merula*) (Miranda et al. 2013) showed a habitat difference in their risk-taking behavior. These findings do not support that urban individuals have increased intrinsic boldness in general or to humans in specific, although we cannot entirely exclude the possibility that the stress from captivity masked the existing intrinsic differences between urban and rural birds.

If the intrinsic boldness of urban and rural birds is similar, it implies that differential colonization and local adaptation may play a less important role in the lower fearfulness of urban individuals. Even if increased boldness to humans has a selective advantage in urban habitats, fear from humans might be part of a behavioral syndrome, in which different behavioral traits are linked by a common underlying (e.g. genetic) cause (Sih et al. 2004a). For example, some urban birds seem to be more fearful of novel situations (Echeverría and Vassallo 2008; Bókony et al. 2012a; Miranda et al. 2013) and of predators (Seress et al. 2011) than their rural conspecifics, both of which suggest selection for a more fearful behavioral type in cities. Thus, if fear from humans is proximally linked with fear from predators and/or novelty, this might constrain their adaptation to opposing selection pressures (Geffroy et al. 2015). Although behavioral syndromes may break down in urban habitats (Scales et al. 2011), we found little evidence for this in house sparrows (Bókony et al. 2012a). Because failing to show anti-predatory response when it is needed is costly (Rödl et al. 2007), urban populations may be selected to maintain a general fear response but fine-tune it within each individual's life through behavioral plasticity. In line with this idea, some studies found that animals have enhanced predator discrimination in populations that experienced higher human disturbance (Carrasco and Blumstein 2012; Cavalli et al. 2016).

In line with this behavioral-plasticity hypothesis, we found that while both urban and rural birds habituated to repeated disturbance by decreasing their hiding response, this habituation was faster in the urban sparrows than in their rural conspecifics. The difference in the habituation potential of urban and rural animals is also supported indirectly by a study on fox squirrels (*Sciurus niger*), where young urban individuals had similar FID and were similarly vigilant as old rural individuals, whereas old urban individuals had shorter FID and were less vigilant, suggesting that urban animals habituated over their lifetime (McCleery 2009). Our analyses showed that the habitat difference in habituation rate is primarily due to reactivity (i.e. the initial response to humans), whereas the recovery rate (i.e. calming down after the disturbance) was similar in urban and rural sparrows. Interestingly, in the only other study we know of that quantified both reactivity and recovery to human disturbance (Ellenberg et al. 2009), the initial heart-rate response of yellow-eyed penguins (*Megadyptes antipodes*) did not change but their recovery times decreased after a habituation period. This suggests that the ways by which animals cope with human disturbance may differ among species.

Habituation is a form of behavioral plasticity, thus it is possible that the faster habituation we found in urban birds is the result of their more flexible behavior. Indeed, it is often assumed that urbanization is accompanied by increased behavioral flexibility (Sih 2013; Sol et al. 2013), a notion that appears notoriously difficult to validate due to controversial empirical evidence and inconsistent interpretations of the term 'behavioral flexibility' (for an overview, see Papp et al. 2015). For example, behavioral flexibility is frequently approximated by foraging innovations (Kark et al. 2007; Møller 2009), but when we measured the problem-solving performance of the same sparrows that were tested for habituation in this paper, we found little difference between urban and rural birds' innovativeness (Papp et al. 2015). This might indicate that behavioral flexibility is context-dependent, such that flexibility in fear responses may not necessarily be linked to flexibility in other behaviors such as foraging techniques.

Several features of urban habitats may contribute to the faster habituation of urban animals. For example, weaker fear response to humans has been found when there were no alternative habitats to flee to (Gill et al. 2001; Gill 2007) or when animals had less access to food resources (Beale and Monaghan 2004a). The distribution of shelter and/or food may be scattered in cities, as suggested by the constrained home range behavior of house sparrows (Vangestel et al. 2010); this might make flight from humans more costly and thus higher tolerance of human disturbance more beneficial. Flock size may also differ between urban and rural habitats, which may then influence behavioral responses to risk (Valcarcel and Fernández-Juricic 2009), for example, by larger flocks spotting the predator from greater distance. It would be interesting to repeat our experiment with birds housed in small flocks to see if we find the same patterns as in the individually-housed birds. Predation risk may also vary along the urban-rural gradient, which may further influence fearfulness; however, no consistent differences were found in house sparrows' fear response to sparrowhawks between rural and urban populations (Seress et al.

2011; Bókony et al. 2012a), not supporting that the slower habituation of the rural birds in the present study was due to habitat differences in predation pressure.

Overall, our results suggest that the weaker fear responses to humans by urban house sparrows are likely to be the result of behavioral plasticity in the form of habituation, whereas we found no evidence for reduced intrinsic boldness in urban compared to rural sparrows. A possible direction for future research is to infer the role of selection and/or differential colonization by separating genetic and environmental effects, i.e. testing whether the differences between urban and rural conspecifics in their behavioral plasticity is due to selection in urban habitats favoring individuals that are intrinsically more flexible in their responses to humans, or due to the animals growing up in habitats with different levels of human disturbance. Recent common garden experiments have started to reveal behavioral differences between urban and rural populations that likely represent genetically based adaptations (Atwell et al. 2012; Miranda et al. 2013); this common garden approach could also be applied to studying variation in behavioral reaction norms (Dingemanse et al. 2010) such as habituation.

CHAPTER 4

DISCRIMINATION BETWEEN DANGEROUS AND NON-DANGEROUS HUMANS[2]

4.1. Introduction

Cities provide a complex and often challenging habitat for wild animals, and various behavioral adjustments seem important for successfully exploiting urbanized environments (Sol et al. 2013). One of the most characteristic aspects of urban environments is frequent proximity to humans, and the animals' ability to cope with this extreme anthropogenic disturbance may play a key role in urban adaptations (Møller 2010a; Carrete and Tella 2011; Sol et al. 2013). For example, as I showed in ***Chapter 3***, animals in more urbanized habitats often show reduced fear reactions, e.g. flee at shorter distances from humans, but also adjust their activities in space and time to avoid disturbance by people (reviewed in Sol et al. 2013). Since humans may present both threat and opportunities such as food, a fine-tuned response to different persons is thought to be beneficial for urban-dwelling animals (Sol et al. 2013).

The ability to individually recognize humans has long been known in domestic animals such as dogs (Racca et al. 2010; Mongillo et al. 2010), sheep (Peirce et al. 2001; Kendrick et al. 2001), rabbits (Davis and Gibson 2000) and homing pigeons (Dittrich et al. 2010; Stephan et al. 2012); for example, the latter two respond differently to people who used to feed them than to familiar or unfamiliar people who never fed them before. Recent studies have also demonstrated such abilities in wild birds that live in urban areas. For example, feral pigeons delayed feeding when food was offered by a previously hostile human (Belguermi et al. 2011), and corvids and mockingbirds attacked persons that previously captured them or approached their nests (Levey et al. 2009; Marzluff et al. 2010; Lee et al. 2011). Since anti-predatory behaviors like vigilance and mobbing may entail high costs of starvation and injury, respectively, individual recognition of humans as potential predators may be adaptive by increasing foraging efficiency and focusing mobbing on hostile persons. Such discrimination may be particularly beneficial for urban animals because higher human population density makes humans a more common as well as more relevant feature of the animals' environment,

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[2] This chapter is a modified version of the research article „Ernő Vincze, Sándor Papp, Bálint Preiszner, Gábor Seress, András Liker & Veronika Bókony (2015): Does urbanization facilitate individual recognition of humans by house sparrows? Animal Cognition 18: 291-298".

and we may also expect a broader range of behaviors from a higher number of people, with a greater possibility for actions towards urban wildlife, both positive (e.g. bird feeding) and negative (e.g. harassment).

Various mechanisms have been hypothesized to explain how the cognitive skills that are necessary for learning to discriminate between individual humans by wild animals may become especially prevalent in urban habitats. Firstly, species with larger brains and more flexible behavior are believed to be pre-disposed for successfully exploiting urban environments (Carrete and Tella 2011; Maklakov et al. 2011; Snell-rood and Wick 2013), and this pre-existing cognitive capacity may also promote individual recognition of humans once the species has colonized urban habitats (Levey et al. 2009; Marzluff et al. 2010; Lee et al. 2011; Sol et al. 2013). Secondly, species without superior cognitive abilities may also establish themselves in cities (Belguermi et al. 2011; Snell-rood and Wick 2013) but once there, urbanized populations may undergo selection for cognitive skills and diverge from rural populations (Snell-rood and Wick 2013). Thirdly, urban animals may develop distinct skills during ontogeny. For example, since animal-human encounters are more frequent in cities, this "pre-exposure to stimuli" throughout the individuals' life may facilitate their differentiation between relevant stimuli, i.e. to detect and learn the distinctive features of humans representing different levels of threat or benefit (Lee et al. 2011).

Either of the above mechanisms or any combination of them may result in a better ability of urban animals to individually recognize people. However, the different combinations of these mechanisms predict varying levels of individual human recognition within species across the urban gradient. If memorizing persons is part of a pre-existing cognitive arsenal of urban-invasive species without further microevolutionary or ontogenetic adaptation, then individuals of such species should be equally good at telling people apart regardless of the type of habitat they live in. In contrast, if this skill evolved or improved specifically in urban populations or results from better learning due to pre-exposure to stimuli, then animals from habitats more densely populated by people should be better at recognizing humans than conspecifics from less populated rural habitats. Previous studies of individual human recognition by wild animals focused only on urban populations (Levey et al. 2009; Marzluff et al. 2010; Belguermi et al. 2011; Lee et al. 2011), and did not compare animals of the same species from differently urbanized habitats.

To test the prediction of the "pre-existing cognitive capacity" hypothesis as opposed to the alternative scenarios, we conducted an experiment on captive house sparrows, a species with long history of commensalism with humans (Anderson 2006; Sætre et al. 2012). House sparrows often exhibit novel behaviors in the wild (Overington et al. 2009; Suárez-Rodríguez et al. 2013) and show remarkable learning skills in lab experiments (Porter 1904; Sasvári 1985), suggesting they may be good candidates for studies on cognition. We captured sparrows from several populations along the urbanization gradient (as described in ***Chapter 3***), and tested experimentally whether they vary in the degree of recognition of and/or responsiveness to individual humans with whom they have different experiences.

Figure 4.1: *Masks used for manipulating the experimenter's appearance in the 3 treatments.*

4.2.Methods

4.2.1. Experimental protocol

Present study was conducted on the same individual sparrows as the study described in ***Chapter 3***. To manipulate the experience of birds associated with different human faces, I manipulated my appearance by wearing different latex masks (Figure 4.1) while playing each of 3 different roles (henceforth: "mask treatment" or "treatment") which represented different levels of threat to the birds, namely "hostile", "non-hostile", and "unfamiliar". For each weekly group of birds (henceforth: "cohorts") a different combination of masks was used from a total of 4 masks, and we randomly distributed the masks between different treatments among the cohorts (Table A4.1); each mask was used for all kind of treatments during the study. I did not change anything else (e.g. clothes) between the treatments on the same day.

The experiment started 1 week after capture. During the first 4 days of the experiment (day 8-11), there were 14 training sessions in total: 7 for non-hostile and 7 for hostile treatment. Each day, an equal number of non-hostile and hostile sessions were performed in randomized order (Table A4.1). In the non-hostile sessions, I came out from cover, and stood 2 m away from the cages facing the birds for 5 minutes, so all the birds could see him. In the hostile sessions I stood 2 m away from the cages for 1 minute, then approached the cages and mimicked an attack against each bird of the cohort in randomized order for 20 seconds each by following the bird with my hand along the cage bars.

On the fifth day, there were 3 test sessions during which I stood 2 m away from the cages for 5 minutes. In each of these test sessions the birds received different mask treatments: I was wearing either the mask representing a non-hostile person, or the mask representing a hostile person, or a third, unfamiliar mask (not seen by the birds before this session) in randomized order (Table A4.1). Henceforth, I will refer to the treatments as “hostile/non-hostile/unfamiliar person”, indicating “the experimenter wearing the mask that represented the hostile/non-hostile/unfamiliar person”. The test sessions were recorded by a video-camera, mounted on a tripod about 2 meters away from the cages.

4.2.2. Quantifying risk taking

I analyzed the birds’ behavior during the 3 test sessions in detail from the video-recordings using Solomon Coder (Péter 2013). The observer was blind to the birds’ capture location and the mask treatment they received. For each bird, position and activity within the cage were recorded as follows. The position of bird was recorded continuously as “hiding” when at least its head was behind the shelter; it was in the “back” when it was not behind the shelter but in the back half of the cage, and in the “front” if it was in the front half of the cage. Activity was only recorded when the bird was not hiding, as “passive” if it did not move for at least 4 seconds, otherwise as “active”. Because the videotaped sessions were slightly different in length, we coded only the first 305 seconds (i.e. the duration of the shortest recording) of each video record.

We quantified risk taking using the following 5 variables (higher values meaning higher level of risk taking):

1. Front: the time the bird spent in the cage’s front part;
2. Not hiding: the time the bird spent outside the shelter (sum of “front” and “back”);
3. Flight latency: the time the bird spent in the cage’s front from the beginning of the session until moving to the back of the cage or behind the shelter (0 for birds that were in the back of the cage or behind the shelter at the beginning of the session);
4. Hiding latency: the latency of the bird to go behind the shelter for the first time (0 for birds that were behind the shelter at the beginning of the session);
5. Passivity: the time the bird spent without moving for at least 4 seconds (i.e. coded as “passive”; excluding the time spent behind the shelter).

We interpreted longer passivity as a higher level of risk taking because in our experiment passive birds were likely more relaxed than active birds, as most activity was fleeing behavior.

Passivity was also positively correlated with the other 4 measures of risk-taking behavior (see Results). All 5 variables were computed separately for each of the 3 test sessions of each bird. Since all response variables measured bold behavior in presence of a human, we computed a single variable from them by rank-transforming them (assigning the lowest rank to the most fearful bird within the session and the highest rank to the least fearful bird) and calculating the mean of these 5 rank scores, separately for the 3 test sessions. This new variable (henceforth "risk taking") shows the birds' average risk taking within a session.

To assess the repeatability of our behavioral measurements, a second observer (Gábor Seress) also coded the behavior of a subset of birds from the video-recordings. We randomly chose 10 5-minute sessions from each of the 3 treatments with at least 1 bird from each cohort, such that no individual was sampled more than once. For these 30 sessions, we calculated the risk-taking score as described above for both observers, and expressed the repeatability between them by the intra-class correlation coefficient (ICC; Nakagawa and Schielzeth 2010).

4.2.3. Statistical analyses

Consistency of behavioral variables between the 3 trials and correlation of behavioral variables with each other were tested by Kendall's concordance tests (Legendre 2005). The effects of mask treatment and habitat were analyzed using linear mixed-effects (LME) models with risk taking as dependent variable. Since there were 3 test sessions for each bird, and the stimulus was presented for all birds in a cohort at the same time, we used bird ID and cohort ID as random factors. We included the following explanatory variables in the initial model: mask treatment (i.e. hostile, non-hostile, or unfamiliar), urbanization category[3] (urban, rural), cage position (vertical and horizontal), treatment order (i.e. order of the 3 treatments over the test day, e.g. non-hostile-hostile-unfamiliar, hostile-unfamiliar-non-hostile, etc.), session number (i.e. first, second, or third), mask ID, food availability (i.e. ad libitum or fasted), sex, and body

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[3] In the published version of this chapter (Vincze et al. 2015), we used a different urbanization score, as the analyses were completed before the *UrbanizationScore* software was available. The scoring method in these analyses was largely the same as described in Chapter 3, but the aerial photographs were scored by a single human observer rather than a software. The urbanization scores from the two methods were strongly correlated with each other (Pearson's correlation coefficient = 0.988). Despite this, the site "Ajka", found in the outskirts of a small town, initially assumed to be an urban site, received a negative urbanization score when scored by a human observer, and thus was treated as a rural site in the analyses of Vincze et al. (2015). However, I consider the urbanization score calculated with the software more reliable, and thus I repeated all analyses with Ajka as an urban site, and present those results in this thesis. Therefore some of the results presented in this chapter quantitatively differ from what was published in Vincze et al. (2015), but the findings are qualitatively unchanged.

condition. We quantified body condition as the scaled mass index proposed by Peig & Green (2009) using the equation of Bókony et al. (2012; 2014). We also included 2 relevant interactions in the initial model, namely the treatment × urbanization interaction to test if the differences between responses to the 3 treatments were different in urban and rural birds, and the treatment order × session number interaction to control for the possible effects of preceding treatments on the same day. From the initial model, non-significant (P>0.05) terms (food availability, sex and body condition) were dropped stepwise, and we report the final model only. We also repeated this analysis by replacing urbanization category with either urbanization score or human population density. To test the pairwise differences of the interaction between mask treatment and urbanization category, we performed post-hoc analyses by calculating linear contrasts and correcting their p-values using the false discovery rate (FDR) method (Benjamini et al. 2001).

4.3. Results

The 5 risk-taking variables were significantly consistent within individuals across the 3 trials (Kendall's concordance tests, not hiding: $W = 0.9$, $P < 0.001$; front: $W = 0.66$, $P < 0.001$; flight latency: $W = 0.52$, $P < 0.001$; hiding latency: $W = 0.68$, $P < 0.001$; passivity: $W = 0.65$, $P < 0.001$; $N = 97$ in all tests), and were positively correlated with each other ($W = 0.48$, $P < 0.001$). Risk taking was also significantly consistent within individuals over the 3 test sessions ($W = 0.79$, $P < 0.001$, $N = 97$). Between the 2 observers, risk taking showed high and significant repeatability ($ICC = 0.913$, $P < 0.001$, $N = 30$).

We found that sparrows responded differently to the 3 masks representing differently threatening persons, and the degree of this discrimination differed between urban and rural birds (mask treatment × habitat interaction; Table 4.1, Figure 4.2). Rural birds behaved more boldly towards the familiar non-hostile person than both the unfamiliar person (linear contrast, $P < 0.001$; $P = 0.001$ after FDR correction) and the familiar hostile person ($P = 0.001$; $P = 0.007$ after FDR correction); there was no difference between their response towards the hostile and the unfamiliar persons ($P = 0.520$; $P = 0.526$ after FDR correction). In contrast, urban birds' risk taking did not differ significantly among the 3 treatments ($P > 0.152$ for all linear contrasts; $P > 0.227$ after FDR correction), whereas they were less bold towards the non-hostile person ($P = 0.004$; $P = 0.013$ after FDR correction), but did not respond differently to the hostile and the unfamiliar persons ($P > 0.076$; $P > 0.151$ after FDR correction) than rural birds. These results are robust since we controlled for several confounding variables in the analyses (Table 4.1) and the effect of mask treatment × habitat interaction on risk taking remained significant when we replaced the urbanization category of each capture site (urban or rural) by either the numeric urbanization score or human population density (Table 4.1; Figure 4.3).

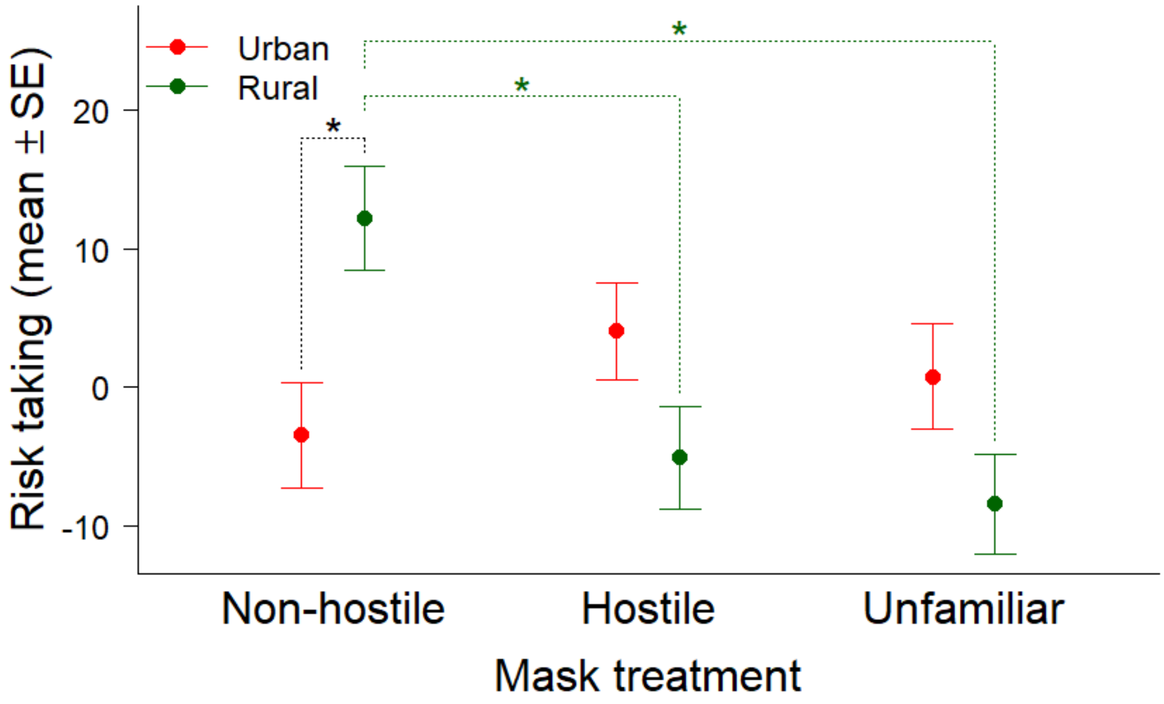

Figure 4.2: *Effects of mask treatment on urban (N=49) and rural (N=48) sparrows' risk taking, shown as residuals controlled for confounding effects. Differences marked by asterisk were significant (*P < 0.05).*

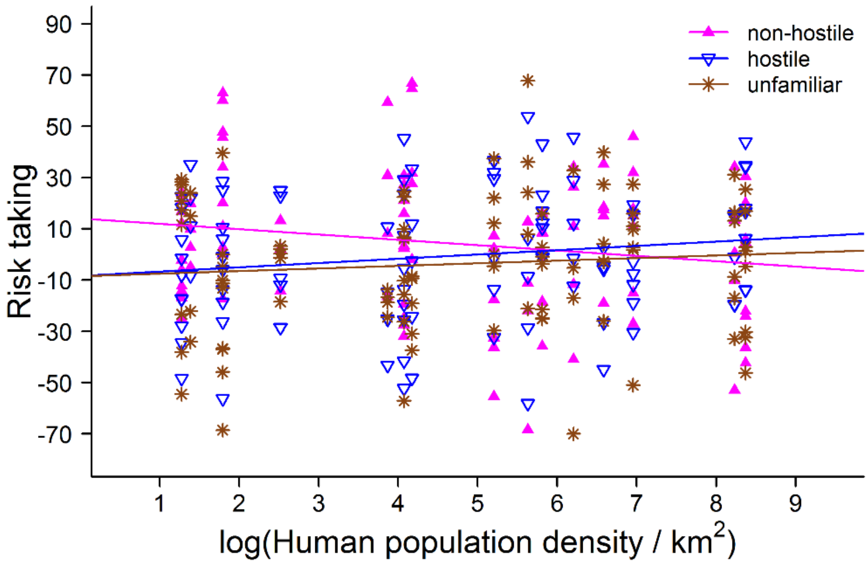

Figure 4.3: *Interactive effects of mask treatment and human population density (on logarithmic scale) on risk-taking (shown as residuals controlled for confounding effects). Lines are regression lines from the final LME model.*

Table 4.1: *Analysis of deviance tables of the final LME models of the risk taking score, using 3 alternative measures of habitat urbanization (urbanization category, urbanization score and human population density; referred to as "urbanization" in the list of predictors). The mask treatment × urbanization interaction, highlighted in bold, expresses the differences between birds from differently urbanized habitats in the extent to which they respond differently to the 3 persons.*

	Urbanization category			**Urbanization score**			**Human population density**		
Predictors	***χ2***	***df***	***P***	***χ2***	***df***	***P***	***χ2***	***df***	***P***
Intercept	77.74	1	< 0.001	77.37	1	< 0.001	65.11	1	< 0.001
Mask treatment	23.71	2	<0.001	9.00	2	0.011	14.81	2	0.001
Urbanization	0.42	1	0.512	1.23	1	0.267	0.88	1	0.348
Mask treatment × Urbanization	**19.35**	**2**	**< 0.001**	**14.26**	**2**	**< 0.001**	**10.43**	**2**	**0.005**
Cage position – vertical	8.15	2	0.017	8.13	2	0.017	8.49	2	0.014
Cage position – horizontal	13.30	4	0.010	12.61	4	0.013	11.71	4	0.020
Mask ID	16.07	3	0.001	11.78	3	0.008	8.50	3	0.037
Treatment order	27.94	4	< 0.001	24.27	4	< 0.001	35.32	4	< 0.001
Session number	6.60	1	0.010	3.34	1	0.068	0.36	1	0.548
Treatment order × Session number	25.05	4	< 0.001	20.96	4	< 0.001	22.70	4	< 0.001

Birds were the least bold in the first test session and became bolder later during the day (Table 4.1); this diurnal change was the steepest when they saw the familiar non-hostile mask in the first session (treatment order × session number interaction, Table 4.1). Birds on the top shelf were bolder than those on the lower shelves, and birds in the middle on each shelf (i.e. those facing the experimenter most directly) were the most fearful (Table 4.1). Overall, the birds behaved more fearfully towards mask B than the other 3 masks (Table 4.1).

4.4. Discussion

Contrary to all hypotheses predicting better individual recognition of humans in urban animals, we found that house sparrows from more urbanized habitats were less discriminating than rural conspecifics in their responses towards persons from whom they had experienced consistently different behaviors. This suggests that urban sparrows either cannot tell persons apart by their faces, or they can but do not adjust their behavior accordingly. We suggest that sparrows' discrimination of, or responsiveness to, individual humans may be constrained in highly urbanized habitats due to increased costs and/or reduced benefits.

Firstly, repeated encounters with the same person might be rare in big cities, so animals may have difficulties with and/or gain less advantage from memorizing individual people. Notably, other wild species that differentiated efficiently among persons (Levey et al. 2009; Marzluff et al. 2010; Belguermi et al. 2011; Lee et al. 2011) were tested mostly in university campuses where the human population, while numerous, might be more constant than at the busy bus/train stations we mostly sampled (Table A3.1). Nevertheless, in these studies only a few negative experiences (Levey et al. 2009) or even a single one (Marzluff et al. 2010) was enough for the birds to efficiently recognize a hostile person, indicating that at least in those species repeated encounters may not be necessary for individual recognition of humans.

Secondly, in more urbanized habitats the interactions between humans and birds might be less diverse, as people may behave more neutrally towards birds, so memorizing different persons may be more rewarding in rural than in urban habitats. This idea is supported by recent studies indicating that both hostile and benevolent human behaviors towards birds are more common in less urbanized areas (Clucas and Marzluff 2012), a higher proportion of people engage in bird feeding at sites with low population density (Fuller et al. 2012), and people in rural areas are better at recognizing endangered birds (Azevedo et al. 2012). Also, house sparrows are often treated as pests in the countryside due to their crop consumption and displacement of other birds (Anderson 2006). Thus rural sparrows, while encountering fewer people overall, may encounter more who are actually worth remembering, both hostile and friendly. The wide-spread use of scarecrows in rural but not in urban areas might have further facilitated the recognition of individual humans, as rural birds may have benefitted from differentiating between these humanlike, but non-hostile dummies and actual, hostile people.

Thirdly, sparrows in urban environments might face some cognitive constraint on learning. For example, pigeons can discriminate between less than a thousand images in an associative learning task (Cook et al. 2005), whereas human population density can exceed several thousand per square-kilometer in cities (Table A3.1), so memory load might prevent urban birds from efficiently learning to recognize people and remembering their attitudes. Although urban species are thought to be cognitively superior (Sasvári 1985; Levey et al. 2009; Marzluff et al. 2010; Lee et al. 2011; Sol et al. 2013), little is known about differences in learning ability between urban and rural conspecifics. Even in species that generally perform well in cognitive tasks, urbanization might suppress the expression of behavioral flexibility by the above mechanisms. For example, a recent study found that cranial capacity, a proxy for brain size, tended to decrease over time in urban populations whereas it increased in rural populations of several mammalian species (Snell-rood and Wick 2013), and smaller brain can result in limited cognitive abilities. Furthermore, another urban species, the Zenaida dove (*Zenaida aurita*) learned more slowly in a foraging task when human disturbance was high (Boogert et al. 2010). Nestling diet for house sparrows is also of lower quality in urban than in rural habitats (Seress et al. 2012). As food quality can influence cognitive development (Lucas et al. 2001; Arnold et al. 2007), this may result in weaker cognitive abilities in urban habitats.

Finally, urban and rural birds might use different cues to tell people apart. In our experiment, only the experimenter's head (face and hair) was manipulated by masks, his height, build, clothing or movements were not. If urban birds pay less attention to the face than rural birds, this may have limited their performance. However, the face is typically a central cue for animals in interactions with humans (Racca et al. 2010; Stephan et al. 2012); for example, dogs prefer to interact with humans with faces oriented towards them and visible eyes (Gácsi et al. 2004) and they differentiate less between their owners and strangers when their heads are covered (Mongillo et al. 2010). Also, birds may view humans as potential predators, and in predator-prey interactions facial orientation and eye-gaze direction may provide vital information about the predator's intentions for the prey (Hampton 1994; Carter et al. 2008). Accordingly, previous studies on birds found that face differences allow effective recognition of human individuals even for long periods (Marzluff et al. 2010) while clothing seems to be a less important cue (Levey et al. 2009; Belguermi et al. 2011; Lee et al. 2011).

Our study highlights the potential for urbanization, and particularly interactions between humans and wild animals, to have intricate effects on the evolution of animal cognition and behavioral flexibility. Differences not only in people's numbers but also the diversity and predictability of their behaviors towards animals may interplay in shaping the pay-offs and constraints of animals' behavioral responses to human disturbance, which is an exciting avenue for further research.

CHAPTER 5:

RISK TAKING TOWARDS SPARROWHAWKS AND HUMANS BY URBAN AND NON-URBAN GREAT TITS[4]

5.1. Introduction

Urban areas differ from natural habitats in a number of ecological characteristics, one of the most obvious being the high abundance of humans. Wild animals usually perceive humans as threat, responding to their proximity with fear and flight (Frid and Dill 2002; Blumstein 2014; Geffroy et al. 2015). Flight behavior has fitness costs, due to energetic expenditure and also because it is in trade-off with other, beneficial behaviors such as foraging and offspring provisioning. Therefore, fleeing is only advantageous if not fleeing is even more costly (Lima 1998; Frid and Dill 2002; Coleman et al. 2008). Humans in cities seldom pose a direct threat to most free-living animals (Clucas and Marzluff 2012), thus reduced fear responses towards humans can be advantageous in urban habitats. Such reduced fear responses have been observed in many urbanized animals (Samia et al. 2015), including birds (Møller et al. 2015; Myers and Hyman 2016; Carrete and Tella 2017), mammals (McCleery 2009; Uchida et al. 2016) and reptiles (McGowan et al. 2014).

There are several mechanisms that can result in lower fear responses in urban compared to non-urban habitats, including population-level mechanisms such as differential colonization of cities and micro-evolutionary adaptation, as well as individual plasticity such as habituation and learning, or a combination of the above processes (Miranda 2017). The relative importance of these mechanisms can vary: some studies suggest that habitat choice based on intrinsic differences is more likely to drive the boldness of urban individuals (Carrete and Tella 2010; Holtmann et al. 2017; Sprau and Dingemanse 2017), while others point towards faster habituation in urban animals (see ***Chapter 3***).

Behaviors in different situations are often driven by the same proximate (e.g. physiological or cognitive) processes, and therefore show a significant covariance across situations; this phenomenon is often called ‘behavioral syndrome’ (Sih et al. 2004a). Fear of humans is often

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[4] This chapter is a modified version of the unpulished manuscript „Ernő Vincze, Veronika Bókony, Ivett Pipoly, Gábor Seress, Bálint Preiszner, Sándor Papp, Brigitta Németh & András Liker: Effects of urbanization on risk taking: general syndrome or threat-specific responses?”.

suggested to be part of a behavioral syndrome of general boldness or risk taking, correlating with aggressiveness (risk taking towards a conspecific opponent; Myers and Hyman, 2016; Scales et al., 2011), neophobia and neophilia (risk taking towards novel stimuli; Bókony et al., 2012; Carrete and Tella, 2017), and anti-predator behavior (risk taking towards non-human predators; Bókony et al., 2012; Carrete and Tella, 2017; Myers and Hyman, 2016). The correlation between responses to humans and responses to non-human predators is often considered particularly strong, as it is often assumed that birds perceive humans as a type of predator (Frid and Dill 2002; Beale and Monaghan 2004b). Consequently, some authors interpret fear responses to humans as a measure of general anti-predator response (Stankowich and Blumstein 2005); for example, they consider the relatively low flight initiation distances (Møller 2012; Jiang and Møller 2017) and less struggle during handling (Møller and Ibáñez-Álamo 2012) by urban compared to non-urban birds as decreased fear from predators . This ‘general risk taking’ hypothesis predicts that if animals reduce their fear from humans in urban habitats, their response to non-human predators will also become weaker (Geffroy et al. 2015).

However, such a correlation between fear of humans and fear of predators may not be adaptive in cities, because generally reduced fear, driven by tolerance to humans, may result in higher mortality by predators if predation pressure is high (i.e. human-mediated behavioral spillover, Geffroy et al. 2015). In such circumstances, urban animals may benefit from ‘breaking down’ the general boldness syndrome and showing differential responses to different types of threat. The ability to recognize distinct types of predators and respond in specific ways to them has been demonstrated in a number of species (Zuberbühler et al. 1997; Greene and Meagher 1998; Zuberbühler 2001; Suzuki 2011; Suzuki 2012). Birds seem to be particularly good at estimating the level of threat by different types of predators and adjusting the intensity of their anti-predator behavior to it (Curio et al. 1983; Templeton et al. 2005; Edelaar and Wright 2006). As humans in urban habitats are seldom hostile with birds (Clucas and Marzluff 2012), whereas non-human predators, particularly those specialized on birds, can still pose a high level of threat, the ‘threat-specific risk taking’ hypothesis predicts that urban birds reduce their fear responses specifically towards humans, while remaining vigilant towards non-human predators.

Notably, the predictions of the general and threat-specific risk taking hypotheses depend on the level of predation pressure in urban habitats. If predation pressure in cities is high, as suggested by empirical studies reporting high predator abundance or high predation risk in urban compared to non-urban habitats (Jokimäki and Huhta 2000; Haskell et al. 2001) or stronger anti-predator behavior in urban than in non-urban populations (Coleman et al. 2008;

Bókony et al. 2012a), urban animals are expected to be bold towards humans but not towards predators. However, other studies found low abundance of predators or low predation risk (McCleery et al. 2008; Møller and Ibáñez-Álamo 2012) as well as weak anti-predator behaviors (McCleery 2009) in urban habitats, suggesting that the effect of urbanization on predation pressure can vary among species or localities, or with other factors such as age (Seress et al. 2011). If predation pressure is low in cities, the threat-specific risk taking hypothesis predicts that urban animals should be bold towards humans and predators alike. Notably, although this latter prediction is identical to what the general risk taking hypothesis predicts irrespectively of the level of predation risk in urban habitats, the underlying mechanisms are different.

Even when predation risk in urban habitats is low, it is still possible to differentiate between the two hypotheses. Instead of comparing the average behavior of animals between urban and non-urban habitats, the correlation between the responses to humans and to non-human predators can be tested within individuals. The general risk taking hypothesis predicts that individuals that are bolder towards humans are also bolder towards predators whether or not the type of habitat is taken into account. In contrast, the threat-specific risk taking hypothesis predicts the within-habitat ‘breakdown’ of this behavioral syndrome because responses to humans and predators should be adjusted independently from each other to the fine-scale variation of danger in the microhabitat of each individual. Two recent studies support the latter hypothesis, i.e. non-urban birds that were more tolerant to humans were also more risk-taking in response to natural predation risk, while urban conspecifics did not show such correlation (Myers and Hyman 2016; Carrete and Tella 2017). In both studies, boldness towards humans was quantified via flight initiation distances (i.e. avoidance), whereas boldness towards predators was quantified by mobbing behavior (i.e. aggression) elicited by a predator dummy or by heterospecific alarm calls. Because urbanization may select for changes in aggressive behaviors (Myers and Hyman 2016, Sprau and Dingemanse 2017), testing whether the avoidance of non-human predators (i.e. a non-aggressive response) is related to avoidance of humans within different habitats could make an important contribution to validating ‘syndrome breakdown’ and thereby understanding how animals adapt to urban environments.

Threat-specific behavior can also go beyond differentiating between humans and non-human predators, as it may also be advantageous to discriminate between individual enemies of the same species, such as individual humans. Although the majority of humans, especially in cities, are neutral towards animals (Clucas and Marzluff 2012), some people still pose a threat towards them by hunting, pest control or by various other forms of repeated disturbance. Under such conditions, it pays off to recognize hostile humans and show increased anti-predator behaviors towards them (Levey et al. 2009; Lee et al. 2011; Nordell et al. 2017) while tolerating other humans and benefitting from the lack of disturbance effects.. Accordingly, differential responses towards differently threatening people have been found in a number of urban-dwelling bird species (Levey et al. 2009; Marzluff et al. 2010; Belguermi et al. 2011; Lee et al. 2011). However, no study to our knowledge has tested whether urban-dwelling individuals are actually better at this discrimination than conspecifics living in non-urban habitats where humans are seldom present (see ***Chapter 4***).

Our present study investigated the behavior of urban and non-urban great tits (*Parus major*), asking four questions: whether urban and non-urban birds i) respond differently to humans; ii) differentiate between familiar and unfamiliar humans to a different extent; iii) respond differently to one of their principal natural predators, the Eurasian sparrowhawk (*Accipiter nisus*); and iv) show correlated responses to humans and sparrowhawks across all birds and within either of the habitat types. Sparrowhawks are relatively small raptors that prey primarily on small passerines, including great tits (Newton and Marquiss 1982; McGrady 1991; Götmark and Post 1996; Zawadzka and Zawadzki 2001) and also frequently breed both in urban and in rural habitats (Thornton et al. 2017).

5.2. Methods

5.2.1. Study species

The great tit (Figure 5.1) is a small (13.7-22.0 g, our unpublished data) insectivorous passerine from the family Paridae. Naturally nesting in cavities of trees, it often breeds in artificial nest boxes, and successfully exploits urban habitats (Gosler and Clement 2007). Compared to the house sparrow, the great tit arrived to anthropogenic habitats more recently, first reported in the cities of Hungary in the 1920s (Møller et al. 2012). The great tit shows biparental care, with the female incubating the eggs for 12-15 days, and then both parents provisioning the nestlings for 18-21 days (Gosler and Clement 2007). Sexes can be distinguished by plumage characteristics, with the males having a broader back stripe on their underside (Gosler and Clement 2007).

Figure 5.1: *Male great tit with color rings. Photograph by Bálint Preiszner.*

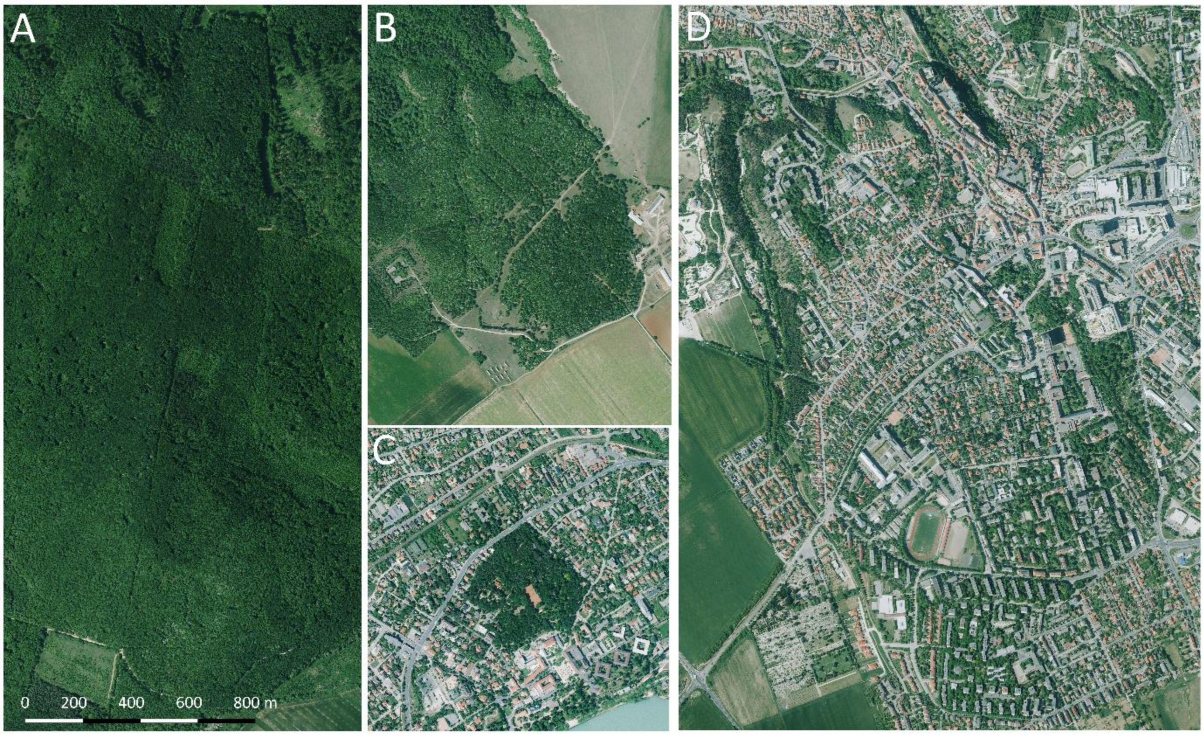

Figure 5.2: *Orthophotos of the two forest sites (A: Szentgál; B: Vilma-puszta) and the two urban sites (C: Balatonfüred; D: Veszprém). The maps are in scale with each other. Acquired in 2015 from the Institute of Geodesy and Remote Sensing of Hungary (Földmérési és Távérzékelési Intézet).*

Great tits are among the most intensely studied birds in the world, thanks to their ubiquity in Eurasia, their tolerance of human disturbance, and their preference for artificial nest boxes. There is excessive literature, among others, on their reproduction (Kuranov 2009; Hedblom and Söderström 2011; Charmantier et al. 2017; Corsini et al. 2017), physiology (Torné-Noguera et al. 2013; Charmantier et al. 2017), antipredator behavior (Curio et al. 1983; Suzuki 2011; Suzuki 2012; Templeton et al. 2016; Davidson et al. 2018), as well as their learning and problem-solving skills (Sasvári 1979; Sasvári 1985; Preiszner et al. 2017). This large amount of existing information, as well as their presence in both extremes of the urbanization gradient, makes them excellent subjects for urbanization studies.

5.2.2. Experimental protocol

This study was conducted as part of a series of field experiments in April to July, 2013 in 4 study sites in Hungary (Bókony et al. 2017; Preiszner et al. 2017). The 2 forest study sites were a beech (*Fagus sylvatica*) and hornbeam (*Carpinus betulus*) forest near Szentgál (47°06’39”N, 17°41’17”E; Figure 5.2A) and a downy oak (*Quercus pubescens*) and South European flowering ash (*Fraxinus ornus*) forest at Vilma-puszta (47°05’02”N, 17°52’01”E; Figure 5.2B), whereas the 2 urban sites were urban parks in the cities of Balatonfüred (46°57’30”N, 17°53’34”E; Figure 5.2C) and Veszprém (47°05’17”N, 17°54’29”E; Figure 5.2D).

At each site we monitored great tits breeding in artificial nest boxes that were placed on trees. Throughout the breeding season, we checked the nest boxes twice a week and recorded the number of eggs and/or nestlings at each visit. When the nestlings were 5-9 days old (day 1 being the day of hatching of the first nestling), we captured one parent with a nest box trap (except for a few pairs where one or both parents had already been ringed). Upon capture, we ringed the birds with a unique combination of a metal ring and 3 plastic colour rings and recorded their sex based on plumage characteristics. The colour rings ensured that we could distinguish between the two parents in the video recordings.

Between days 6 and 16 of nestling age we conducted 5 behavioral tests at each nest, recorded by a camera (GoPro Hero 2; 7 × 5.5 × 5 cm). The camera was concealed in a black plastic box that was 15 cm from the nest entrance and was permanently attached to the nest box, installed before the breeding season so the birds were already familiar with its presence. In a former experiment we have validated that this box hid the camera effectively, as further familiarization to the camera did not have any effect on the parent birds’ return latency after nest disturbance and their number of nest visits (Seress et al. 2017). The first 3 of the 5 behavioral tests, investigating neophobia and problem solving, are described in detail in

Preiszner et al. (2017). Each of these 3 tests began with a 30-minute baseline observation period to measure 2 behavioral variables: the birds' latencies to first return to their nests after the short disturbance at their nest (i.e. camera instalment), and the number of consecutive nest visits, which were almost exclusively feeding events (i.e. bringing food for the nestlings). For the present study, we only used data from the 30-min baseline observations of these first 3 tests (see below). The fourth and fifth tests, analyzed in detail here, quantified the birds' responses to humans and to sparrowhawk, also measured as their return latency and number of consecutive nest visits. These 2 tests took place between day 8 and 16 (mean ± *SD* = 12.6 ± 1.6) of nestling age, in randomized order, each on a different day. Both tests consisted of 3 main phases (Figure 5.3): a 15 minutes long (mean ± *SD* = 932 ± 77 sec) pre-stimulus phase and 2 test phases, each 20 minutes long (1224 ± 52 sec and 1237 ± 59 sec for the first and the second test phase respectively). Both test phases were further divided into 2 equal-length periods: the first with a stimulus present (stimulus period) and the second after removing the stimulus (post-stimulus period, see below).

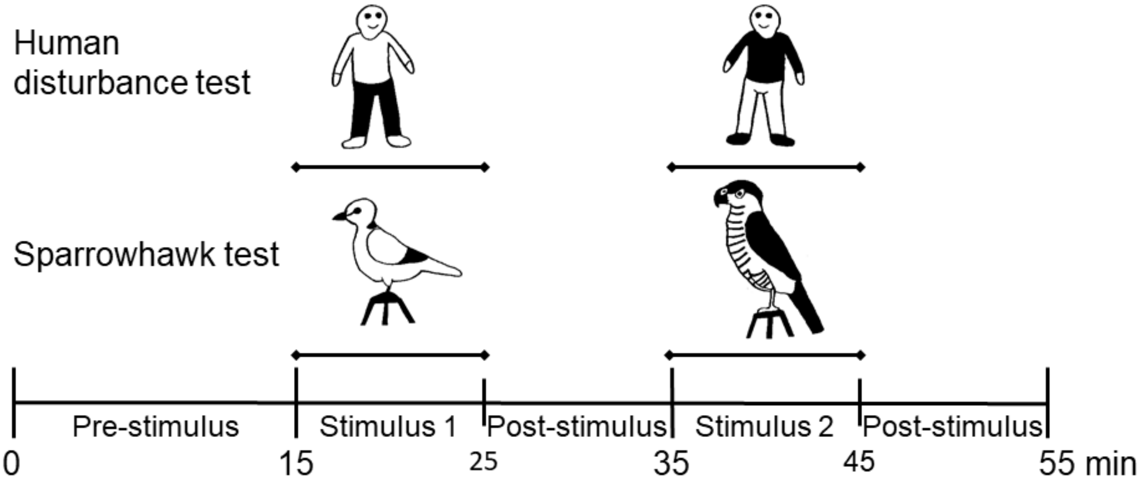

Figure 5.3. *Schematic of the test protocols. Sketches by the author.*

5.2.2.1. Human disturbance test

At the beginning of the pre-stimulus phase, the experimenter checked the nest content, placed the camera in the hiding box, started the recording, and left the vicinity of the nest for the entire duration of the test. Both test phases (Figure 5.3) started with a stimulus period during which one person was standing under the nest box, but not looking at it, for 10 minutes (595 ± 24 sec), followed by a 10-minute long (638 ± 73 sec) post-stimulus period during which no person was standing under the nest box or in its vicinity. 2 different persons were present in the 2 stimulus periods. One person was 'familiar hostile', i.e. someone who regularly checked the nest box (6 to 15 times, mean ± *SD* = 11.74 ± 1.63, from egg laying until the human disturbance test) and participated in the trapping of one parent, and therefore the birds could view them as potentially dangerous and get sensitized to them. For other passerines, even 4 nest checks were enough to specifically recognize the person who checked the nest (Levey et al. 2009). The other person was 'unfamiliar', i.e. someone who never visited the vicinity of the nest before the test. The stimulus persons were of varying gender, build, clothing and hairstyle; the familiar persons, i.e. the researchers conducting the field work, also wore various clothes during nest checks. The order of the 2 persons was randomized between the 2 test phases. Both persons announced their arrival and their departure audibly to the camera, thereby the start and end of each stimulus phase was identifiable from the video recordings.

5.2.2.2. Sparrowhawk test

The sparrowhawk test followed a protocol largely similar to the human disturbance test (Figure 5.3). Before checking the contents of the nest box and starting the pre-stimulus phase, the experimenter placed a tripod below the nest box, with the tripod's top ca. 3 m away from the entrance, which remained there until the end of the test. We considered this distance short enough for the birds to perceive approaching and entering the nest box in presence of the stimulus as risky. The first test phase was a 'dove' phase, during which a mounted collared dove (*Streptopelia decaocto*) was present on the tripod for the 10 minutes of the stimulus period (608 ± 42 sec), whereas the second test phase was a 'sparrowhawk' phase during which a mounted sparrowhawk was present on the tripod for the 10 minutes of the stimulus period (611 ± 33 sec). Both stimuli were followed by a 10-minute (627 ± 36 sec) post-stimulus period, during which no dummy was present on the tripod. The order of the 2 stimuli were fixed, with the dove always preceding the sparrowhawk. We decided on fixed order because we expected the sparrowhawk to be a lot more threatening than the collared dove, and thus there would be strong carry-over effects in the second phase if the sparrowhawk was presented first (Bell 2013). We used the collared dove as control because it is a granivorous species (thus not perceived by tits as potential predator) that is common in both urban and rural habitats in Hungary, and is close in size to the sparrowhawk. We had 2 dove and 2 sparrowhawk mounts, which were randomly alternated between tests. At the start and end of each stimulus period, the placement and the removal of the mount was announced audibly by the experimenter.

5.2.3. Statistical analyses

We only used data from tests conducted with the first annual brood of each pair, because seasonal effects can influence nest defense behavior in great tits (Curio et al. 1984), and we had too few data from second broods to statistically control for seasonal effects. Out of 122 behavioral tests from first broods, we excluded 9 human disturbance tests and 13 sparrowhawk tests from the analyses due to technical problems, i.e. poor image or sound quality, , the test was terminated prematurely due to camera failure, or the stimulus was present for less than 8 minutes or more than 12 minutes. We chose the latter cut-off points because this way we included the majority of the tests, excluding only 1 extremely short (<7 minutes) stimulus period in the human disturbance test and 3 extremely long (>13 minutes) stimulus periods in the sparrowhawk test. Furthermore, we also excluded 25 individuals that never appeared on the video over the course of the entire test, and 15 individuals that were inside the nest at the start of the stimulus period and did not emerge for more than 2 consecutive minutes (i.e. were exposed to the stimulus for less than 8 minutes). Thus, we analyzed the data of 47 males and 39 females from 50 nesting attempts in the human disturbance test, and 40 males and 34 females from 43 nesting attempts in the sparrowhawk test.

We quantified the individuals' behavior in each phase using 2 variables: return latency and number of nest visits. Both variables were calculated for the pre-stimulus phase and the 2 test phases, i.e. in the test phases we did not calculate separate return latencies and nest visits for the stimulus and post-stimulus periods. We did this because during the stimulus period, the majority of birds did not enter the nest box (83.7% of birds in both stimulus periods of the human test; 68.9% of birds in the stimulus period of the sparrowhawk phase), therefore there was too little variation in the behaviors in the stimulus periods formeaningful analyses of this period separately. Nest visits were defined as the events when a bird entered the nest box. Return latencies were defined as the time elapsed between the start of the phase and the bird's first nest visit in the phase, regardless whether it was in the stimulus or the post-stimulus period. This is justified because birds that return to the nest in presence of the stimulus can be considered bolder than birds that return after the removal of the stimulus. Birds that did not visit the nest until the beginning of the next test phase or the termination of the test were assigned maximal latencies (20 minutes for pre-stimulus phase, 25 minutes for test phase, to ensure that they are longer than the longest possible test phase; note that these maximal latencies were used as censored observations in the analyses, as explained below). Similarly, in the test phases the number of nest visits was the sum of visits in the stimulus and the post-stimulus period. We assumed that longer latencies and fewer nest visits indicate lower level of risk taking, i.e. a stronger fear from the stimulus. Although the 2 variables are not independent from each other, as birds with high return latencies would likely have fewer nest visits, we decided to analyze the 2 variables in separate models, because combining them in a principal component analysis would not allow appropriate treatment of the birds that did not visit the nest in a test phase (see below).

Because return latencies and nest visit frequencies may be influenced by factors other than fear elicited by the test stimuli, we considered several potentially confounding variables. From the 3 × 30 minutes of baseline observation of the first 3 tests recorded 1 to 7 (mean ± *SD* = 2.93 ± 1.56) days before the human disturbance and sparrowhawk tests (see above), we calculated each bird's average return latency (birds that had not returned to the nest during the 30 minutes were given a latency of 3600 sec) and average number of nest visits over 30 minutes (henceforth 'baseline return latency' and 'baseline nest visit number'). Both return latency and number of nest visits had low, but significant repeatability over these three baseline observations (intra-class correlation coefficient tests: return latency: ICC = 0.307; $F_{102,206} = 2.33$; $p < 0.001$; number of nest visits: ICC = 0.274; $F_{102,206} = 2.13$; $p < 0.001$). We included these variables in the analyses because they measure the birds' provisioning behavior when no threatening stimulus (tripod, mount, or human) was present at the nest (apart from the very short presence of the experimenter at the beginning of the test to start the camera), which is likely influenced by persistent constraints. This baseline provisioning behavior is likely to be influenced by persistent constraints such as territory quality in regards of food (Tremblay et al. 2005) and intrinsic foraging abilities of the parents (Cole et al. 2012). As trapping is known to affect the nest visitation behavior of tits (Seress et al. 2017), we included trapping status (i.e. whether an individual bird was trapped or not before the test) in our analyses. We also included the length of the stimulus period (i.e. the time the mount or human was present at the nest; henceforth: stimulus length), to control for the slight variation in this variable among tests, as well as the number of nest checks preceding the human disturbance test, to control for how familiar the birds were with the human.

All analyses were run in R (version 3.3.0; R Core Team 2016), using the 'car' (Fox et al. 2010), 'MASS' (Venables and Ripley 2002), 'nlme' (Pinheiro et al. 2009), 'coxme' (Therneau 2012) and 'lsmeans' (Lenth 2016) and 'irr' (Gamer et al. 2017) packages. To analyze return latencies, we built Cox's mixed-effects proportional hazards models, with maximal latencies used as censored observations, whereas the numbers of nest visits were analyzed with generalized mixed-effects models with quasi-Poisson error distribution and log link function. In both types of models, the units of analysis were the test phases (i.e. two 20-minute phases per bird per test). In all our models, we used bird ID nested in pair ID as random factors. For each of our 4 research questions (see below), we included site as a fixed effect in the model, and tested the effect of urbanization by a linear contrast between the 2 urban versus the 2 rural sites. We used this approach rather than including habitat as a fixed effect and site as a random effect because variance estimations of random effects with few levels are unreliable (Piepho et al. 2003). Similarly, we cannot use both site and habitat as fixed effects because site is contained within habitat (Piepho et al. 2003). Note that our approach also treats nests from the same site as non-independent, thus pseudoreplication is controlled for. Furthermore, we added a set of potentially confounding variables into each model; then we removed the statistically non-significant confounding variables with $P > 0.1$ via stepwise backwards model selection, and tested the effect of habitat in the final model that contained only the statistically significant ($P < 0.05$) and marginally non-significant ($0.05 < P < 0.1$) confounding variables beside the habitat effect. The linear contrasts to estimate habitat effect were always calculated from these final models. The full models, including all potential confounding variables, and the model diagnostic plots of the final models, are presented in the supplementary material (Table A5.1 A-H, Figure A5.1 A-H). The analyses of each research question are detailed below.

5.2.3.1. Responses to human disturbance

To express the birds' response to the presence of humans (regardless whether they are familiar or unfamiliar; see Results), first we built a model with return latency (or number of nest visits) in the test phases (2 phases per bird) as dependent variable and return latency (or number of nest visits) in the pre-stimulus phase as fixed effect (covariate). This model contained no random factors because it was not used for significance testing but for estimating the relationship between the individuals' behaviors in non-disturbed and disturbed situations. We extracted the residuals for each bird in each test phase from this model, which we, henceforth, refer to as the birds' 'response to human disturbance'. Larger positive residuals mean that the individual was bolder (returned earlier to the nest or visited the nest more frequently) upon disturbance than predicted by its non-disturbed, pre-stimulus behaviors, whereas more negative values mean lower than expected risk taking (thus, in the case of return latency, larger residuals belong to shorter latencies; however, we will refer to this variable as "residual return latency" to maintain consistent variable names across the four questions). In the subsequent analyses we used these residuals as the dependent variable to test the effect of habitat in a linear mixed-effects model containing site as a fixed factor. Additionally, we tested the potentially confounding effects of sex, trapping status, nest height, number of nestlings, age of nestlings, stimulus length, calendar date, time of day, number of nest checks, phase (first or second person), and phase × site interaction for a possible difference in habituation rates between habitats. To test the effect of habitat, we estimated the least-squares means of the dependent variable for each of the 4 sites, and calculated the linear contrast between the 2 urban versus the 2 forest sites.

5.2.3.2. Responses to hostile versus unfamiliar humans

In these analyses, we compared the birds' behavior in the 'familiar' and 'unfamiliar' test phases of the human disturbance test (expressed by the term 'person' in the models), and tested whether the difference between the 2 phases (henceforth: 'response to hostile versus unfamiliar humans') differs between habitat types, by including the person × site interaction in the model. Additionally, we tested the potentially confounding effects of sex, trapping status, nest height, number of nestlings, age of nestlings, stimulus length, calendar date, time of day, number of nest checks, baseline return latency (or baseline nest visit number) and pre-stimulus return latency (or pre-stimulus nest visit number), the person × trapping interaction (to test whether trapped birds, which had a stronger negative experience with the familiar hostile person, were better at discriminating between people) and the person × phase × site interaction; by the latter we aimed to test whether differentiation between persons depended on the order the people were presented, and whether this differs between sites. From these models, we estimated least-squares means of the dependent variable for each person–site combination, and then calculated the unfamiliar–familiar differences (i.e. the responses to hostile versus unfamiliar humans) as linear contrasts for each site. Finally, we calculated a single linear contrast of the latter response between urban versus forest sites.

5.2.3.3. Responses to sparrowhawk

In these analyses, we compared the dove phase and the sparrowhawk phase (included by the term 'stimulus' in the models), and tested whether the difference between the 2 phases (henceforth: 'response to sparrowhawk') varies with habitat, by including the stimulus × site interaction in our models. Additionally, we tested the potentially confounding effects of sex, trapping status, nest height, number of nestlings, age of nestlings, stimulus length, calendar date, time of day, baseline return latency (or baseline nest visit number) and pre-stimulus return latency (or pre-stimulus nest visit number). From these models, we estimated least-squares means of the dependent variable for each stimulus–site combination, and then calculated the dove–sparrowhawk differences (i.e. responses to sparrowhawk) as linear contrasts for each site.

Finally, we calculated a single linear contrast of the responses to the sparrowhawk between urban versus forest sites.

5.2.3.4. Correlation between responses to humans and sparrowhawk

To test whether the responses to humans correlate with the responses to sparrowhawk, we used a subset of birds ($N = 55$) for which we had data from both tests. As in the analysis of our first question (see above), we expressed the birds' response to human disturbance (regardless whether they were familiar or unfamiliar) by taking the residuals from a model with return latency (or numbers of nest visits) in the test phases (2 phases per bird) as dependent variable and pre-stimulus return latency (or pre-stimulus number of nest visits) as fixed effect (covariate), without random factors. To similarly express the birds' response to sparrowhawk, we built a model with return latency (or number of nest visits) in the sparrowhawk phase as dependent variable and return latency (or number of nest visits) in the dove phase as fixed effect (covariate), and then extracted the residuals (1 for each bird) from this model. To test whether there was a linear relationship between responses elicited by the two types of threat across all birds, we built a linear mixed-effects model with residual return latency (or residual number of nest visits) in the human disturbance test as the dependent variable (2 data points per bird) and residual return latency (or residual number of nest visits) in the sparrowhawk test as fixed effect (covariate). We tested whether the correlation differs among sites using a similar model that also included site as fixed factor and its interaction with the covariate. Additionally, we tested the potentially confounding effects of sex, trapping status, nest height, number of nestlings, age of nestlings, stimulus length, and phase (first or second person). From these models, we estimated the slope of regression for each site, and we compared the urban slopes with the forest slopes by calculating a single linear contrast.

5.3. Results

5.3.1. Responses to human disturbance

In the test phases with humans, return latencies were shorter and nest visits were more frequent in urban than in forest sites (Table 5.1, Figure 5.4, Figure A5.2). This habitat difference in responses to human disturbance was statistically significant both for return latencies and for the number of nest visits (Table 5.1). Trapped birds and birds with fewer nestlings returned later and visited the nest less frequently than non-trapped birds and those with more nestlings (Table 5.1). Return latency also showed a trend to be shorter later in the day (Table 5.1A).

Table 5.1. *Parameter estimates for fixed and random effects of the final models with only significant and marginally non-significant variables and urban-rural differences (linear contrasts) in responses to human disturbance by great tits (sample size: 86 individuals of 50 pairs). Responses were measured as residual return latencies (A) or nest visit numbers (B), controlled for pre-stimulus return latencies or pre-stimulus numbers of nest visits. Positive contrasts indicate that urban birds had shorter return latencies or higher number of nest visits than rural birds.*

A) Return latencies

Fixed effects	**Estimate ± *SE***	***df***	***t***	***P***
Site – Szentgál	-1.948 ± 0.607	44	-3.21	0.003
Site – Balatonfüred	-0.992 ± 0.438	44	-2.26	0.029
Site – Veszprém	-0.959 ± 0.452	44	-2.12	0.040
Site – Vilmapuszta	-1.701 ± 0.609	44	-2.79	0.008
Trapping status – Trapped	-0.414 ± 0.141	36	-2.93	0.006
Nestling number	0.100 ± 0.042	44	2.41	0.020
Time of day (minutes)	0.001 ± 0.000	44	1.99	0.053
Random effects	***SD***			
Nest ID	<0.001			
Bird ID in Nest ID	0.416			
Residual variance	0.653			
Contrast: urban vs rural	**Contrast ± *SE***		***t***	***P***
	0.849 ± 0.253		3.35	0.002

B) Number of nest visits

Fixed effects	**Estimate ± *SE***	***df***	***t***	***P***
Site – Szentgál	-1.904 ± 0.842	45	-2.26	0.029
Site – Balanonfüred	-1.260 ± 0.500	45	-2.52	0.015
Site – Veszprém	-0.628 ± 0.573	45	-1.10	0.279
Site – Vilma-puszta	-1.854 ± 0.820	45	-2.26	0.029
Trapping status – Trapped	-0.917 ± 0.237	36	-3.87	<0.001
Nestling number	0.146 ± 0.070	45	2.09	0.042
Random effects	***SD***			
Nest ID	<0.001			
Bird ID in Nest ID	0.763			
Residual variance	1.013			
Contrast: urban vs rural	**Contrast ± *SE***		***t***	***P***
	0.935 ± 0.420		2.23	0.031

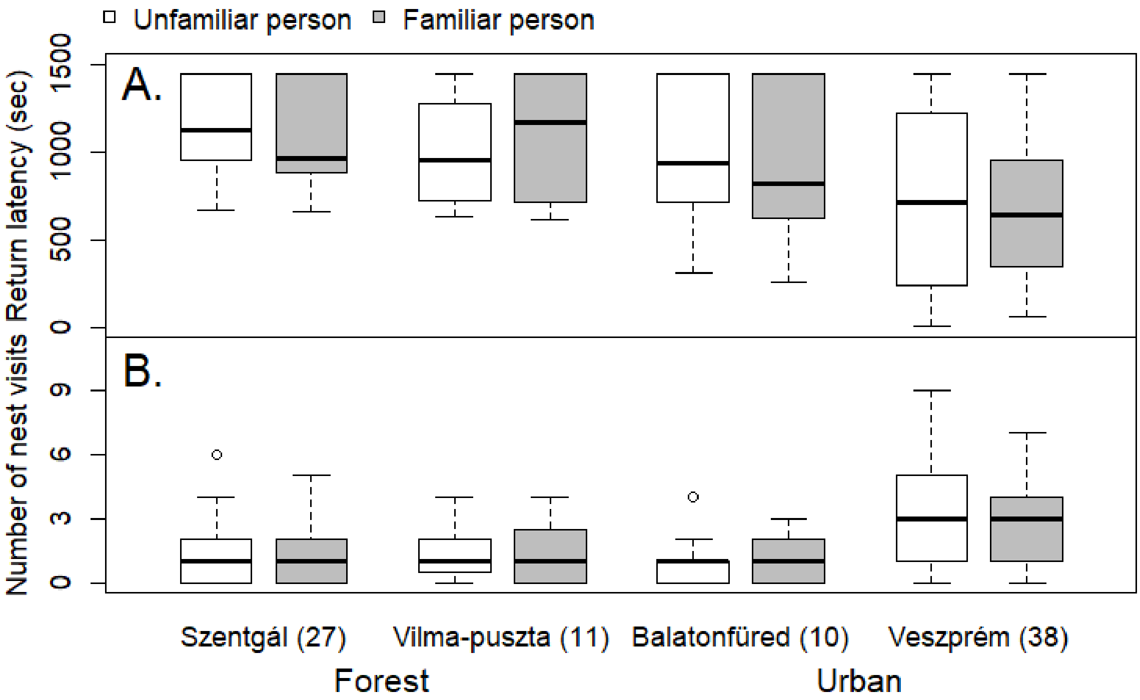

Figure 5.4. *Return latencies (A) and numbers of nest visits (B) in the human disturbance test at the 4 sites. Sample sizes for each site (number of individual birds) are provided in brackets. Boxplots show the median and the interquartile range, with the whiskers representing data within the 1.5 × interquartile range.*

5.3.2. Responses to hostile versus unfamiliar humans

There were no significant responses to hostile versus unfamiliar humans in any of the 4 sites, i.e. return latencies and numbers of nest visits did not differ between the familiar and unfamiliar persons' phases (Table 5.2). Therefore, there was no significant difference between urban and forest habitats in the response to hostile versus unfamiliar humans (Table 5.2, Figure 5.4). In case of return latencies, there was a marginally non-significant phase × person interaction (Table 5.2A): in the second test phase, latencies tended to be shorter when the person was familiar, whereas in the first test phase the latencies were relatively long irrespective of the person's identity (Table A5.2; Figure A5.3). Trapped birds returned later and visited the nest less frequently than non-trapped birds. Birds with more nestlings returned earlier to the nest; nest visit rates in the test phase positively correlated with baseline and, as a trend, pre-test visit rates.

Table 5.2. *Parameter estimates and random effects of the final models with only significant and marginally non-significant variables, within-site linear contrasts between behavior in the test phases with the unfamiliar and familiar persons (responses to hostile versus unfamiliar humans), and urban-rural differences (linear contrasts) in these responses), testing recognition of individual humans by great tits (sample size: 86 individuals of 50 pairs).*

A) Return latencies.

Fixed effects	**Estimate[b] ± *SE***	**exp(Estimate)**	***z***	***P***
Site[a] – Balatonfüred	2.080 ± 0.900	8.007	2.31	0.021
Site[a] – Veszprém	2.886 ± 0.610	17.927	4.73	0.000
Site[a] – Vilmapuszta	1.467 ± 0.634	4.338	2.32	0.021
Person – Familiar	-0.194 ± 0.513	0.824	-0.38	0.710
Phase – Second	-0.543 ± 0.396	0.581	-1.37	0.170
Trapping status – Trapped	-1.069 ± 0.339	2.913	3.15	0.002
Nestling number	0.268 ± 0.098	1.307	2.72	0.007
Site:Person – Balatonfüred:Familiar	0.207 ± 0.723	1.230	0.29	0.770
Site:Person – Veszprém:Familiar	-0.155 ± 0.480	0.856	-0.32	0.750
Site:Person – Vilmapuszta:Familiar	-0.858 ± 0.673	0.424	-1.28	0.200
Person:Phase – Familiar:Second	1.265 ± 0.672	3.544	1.88	0.060
Random effects	***SD***			
Nest ID	0.143			
Bird ID in Nest ID	1.127			
Contrasts: unfamiliar vs familiar				
Site	**Contrast[c] ± *SE***		***z***	***P***
Szentgál	-0.439 ± 0.378		-1.16	0.677
Vilma-puszta	0.420 ± 0.552		0.76	0.906
Balatonfüred	-0.646 ± 0.637		-1.01	0.774
Veszprém	-0.283 ± 0.289		-0.98	0.795
Contrast of contrasts: urban vs rural	**Contrast[d] ± *SE***		***z***	***P***
	-0.455 ± 0.477		-0.95	0.340

[a] *For the factor 'Site', Szentgál is the reference level.*

[b] *Parameter estimates are shown on logit scale (Cox models; note that larger parameter values indicate shorter return latency.*

[c] *Contrasts are expressed as logits of hazard ratios in Cox models. Larger positive values indicate shorter latencies in the unfamiliar person phase and/or longer latencies in the familiar person phase. P-values were adjusted with the Tukey method.*

[d] *Positive contrasts indicate that the difference between the response to the familiar person versus the unfamiliar person was more positive (or less negative) than in rural birds, i.e. urban birds had either longer latencies in the familiar person phase, or shorter latencies in the unfamiliar person phase.*

B) Number of nest visits

Fixed effects	**Estimate[a] ± *SE***	***df***	***t***	***P***
Site – Szentgál	-0.361 ± 0.259	46	-1.39	0.170
Site – Balatonfüred	-0.500 ± 0.374	46	-1.34	0.188
Site – Veszprém	0.285 ± 0.234	46	1.22	0.230
Site – Vilmapuszta	-0.328 ± 0.359	46	-0.91	0.366
Person – Familiar	0.241 ± 0.231	83	1.05	0.299
Trapping status – Trapped	-0.434 ± 0.177	34	-2.45	0.019
Pre-test nest visit number	0.092 ± 0.049	34	1.90	0.066
Baseline nest visit number	0.133 ± 0.034	34	3.95	<0.001
Site:Person – Balatonfüred:Familiar	-0.241 ± 0.481	83	-0.50	0.618
Site:Person – Veszprém:familiar	-0.305 ± 0.266	83	-1.14	0.256
Site:Person – Vilmapuszta:familiar	-0.241 ± 0.429	83	-0.56	0.576
Random effects	***SD***			
Nest ID	<0.001			
Bird ID in Nest ID	0.391			
Residual variance	0.959			
Contrasts: unfamiliar vs familiar				
Site	**Contrast[b] ± *SE***		***t***	***P***
Szentgál	-0.241 ± 0.231		-1.05	0.758
Vilma-puszta	0.000 ± 0.362		0.00	1.000
Balatonfüred	0.000 ± 0.423		0.00	1.000
Veszprém	0.063 ± 0.133		0.48	0.983
Contrast of contrasts: urban vs rural	**Contrast[c] ± *SE***		***t***	***P***
	0.152 ± 0.308		0.49	0.623

[a] *Parameter estimates are shown on natural-base logarithmic (quasi-Poisson models).*

[b] *Contrasts are expressed as natural-base logarithms of differences in quasi-Poisson models. Larger positive values indicate higher numbers of nest visits in the unfamiliar person phase and/or longer latencies and lower numbers of nest visits in the familiar person phase. P-values were adjusted with the Tukey method.*

[c] *Positive contrasts indicate that the difference between the response to the familiar person versus the unfamiliar person was more positive (or less negative) than in rural birds, i.e. urban birds had lower numbers of nest visits in the familiar person phase, or higher numbers of nest visits in the unfamiliar person phase.*

5.3.3. Responses to sparrowhawk

Return latencies were longer and nest visits were fewer in the sparrowhawk phase than in the dove phase at all 4 sites (Figure 5.5); these responses were statistically significant in Veszprém and Szentgál (the sites with largest sample size) and, for the number of nest visits, marginally non-significant in the Vilma-puszta forest site (Table 5.3). These results support that great tits perceived sparrowhawk mounts more dangerous than the non-predatory dove mounts. Return latencies and numbers of nest visits did not significantly differ between urban and forest birds in the dove phase (Table A5.3), whereas in the sparrowhawk phase forest birds had significantly longer return latencies but not fewer nest visits than urban birds (Table A5.3). Responses to sparrowhawk showed a marginally non-significant trend to be greater in forest than in urban habitats for both latency and number of nest visits, meaning that forest birds delayed their return and reduced nest visitation frequency in the sparrowhawk phase compared to the dove phase to a greater extent than urban birds did (Table 5.3, Figure 5.5). Birds with more nestlings returned earlier and visited their nests more frequently than birds with fewer nestlings. Return latency increased and nest visit rate decreased over the day. Birds breeding later in the season tended to return to their nests later than those breeding earlier. Nest visit rate in the test phases were positively correlated with nest visit rate in the baseline observations.

Table 5.3. *Parameter estimates and random effects of the final models with only significant and marginally non-significant variables, responses to sparrowhawk (i.e. linear contrasts between the dove phase and the sparrowhawk phase) in each site, and urban-rural differences (linear contrasts) in these responses by great tits (sample size: 74 individuals from 43 pairs).*

A) Return latencies

Fixed effects	**Estimate[b] ± *SE***	**exp(Estimate)**	***z***	***P***
Site[a] – Balatonfüred	0.975 ± 0.627	2.652	1.56	0.120
Site[a] – Veszprém	0.809 ± 0.466	2.245	1.74	0.083
Site[a] – Vilmapuszta	-0.117 ± 0.634	0.889	-0.19	0.850
Phase – Sparrowhawk	-2.361 ± 0.518	0.094	-4.56	0.000
Nestling number	0.177 ± 0.069	1.193	2.56	0.010
Calendar date	-0.035 ± 0.019	0.966	-1.79	0.073
Time of day (minutes)	-0.001 ± 0.001	0.999	-1.86	0.062
Site:Phase – Balatonfüred:Sparrowhawk	1.658 ± 0.74	5.248	2.24	0.025
Site:Phase – Veszprém:Sparrowhawk	1.533 ± 0.579	4.634	2.65	0.008
Site:Phase – Vilmapuszta:Sparrowhawk	1.113 ± 0.934	3.042	1.19	0.230
Random effects	***SD***			
Nest ID	0.456			
Bird ID in Nest ID	0.020			
Contrasts: unfamiliar vs familiar				
Site	**Contrast[c] ± *SE***		***z***	***P***
Szentgál	2.361 ± 0.518		4.56	<0.001
Vilma-puszta	0.703 ± 0.532		1.32	0.561
Balatonfüred	0.828 ± 0.279		2.96	0.012
Veszprém	1.248 ± 0.783		1.60	0.375
Contrast of contrasts: urban vs rural	**Contrast[d] ± *SE***		***z***	***P***
	-1.039 ± 0.555		-1.87	0.061

[a] *For the factor ‘Site’, Szentgál is the reference level.*

[b] *Parameter estimates are shown on logit scale (Cox models; note that larger parameter values indicate shorter return latency).*

[c] *Contrasts are expressed as logits of hazard ratios in Cox models. More positive values indicate stronger responses (i.e. greater increase in latency from the dove phase to the sparrowhawk phase). P-values have been adjusted with the Tukey method.*

[d] *Negative contrasts indicate that urban birds responded less strongly to the sparrowhawk than rural birds, i.e. the difference between the return latencies in the dove and sparrowhawk phases was smaller for urban than for rural birds.*

B) Number of nest visits

Fixed effects	**Estimate^a ± *SE***	***df***	***t***	***P***
Site – Szentgál	-0.238 ± 0.730	37	-0.33	0.746
Site – Balatonfüred	0.176 ± 0.579	37	0.30	0.763
Site – Veszprém	0.597 ± 0.565	37	1.06	0.297
Site – Vilmapuszta	-0.073 ± 0.786	37	-0.09	0.926
Phase – Sparrowhawk	-1.713 ± 0.414	71	-4.14	0.000
Nestling number	0.127 ± 0.056	37	2.27	0.029
Baseline nest visit number	0.125 ± 0.037	31	3.35	0.002
Time of the day (minutes)	-0.001 ± 0.000	37	-2.37	0.023
Site:Phase – Balatonfüred:sparrowhawk	0.979 ± 0.607	71	1.61	0.111
Site:Phase – Veszprém:sparrowhawk	1.102 ± 0.446	71	2.47	0.016
Site:Phase – Vilmapuszta:Sparrowhawk	0.440 ± 0.681	71	0.65	0.520
Random effects	***SD***			
Nest ID	0.177			
Bird ID in Nest ID	0.399			
Residual variance	1.217			
Contrasts: unfamiliar vs familiar				
Site	**Contrast^b ± *SE***		***t***	***P***
Szentgál	1.713 ± 0.414		4.14	<0.001
Vilma-puszta	0.734 ± 0.444		1.65	0.352
Balatonfüred	0.611 ± 0.166		3.67	0.002
Veszprém	1.273 ± 0.541		2.35	0.083
Contrast of contrasts: urban vs rural	**Contrast^c ± *SE***		***t***	***P***
	-0.820 ± 0.415		-1.98	0.052

[a] Parameter estimates are shown on natural-base logarithmic scale (quasi-Poisson models).

[b] Contrasts are expressed as natural-base logarithms of differences in quasi-Poisson models. More positive values indicate stronger responses (i.e. greater i decrease in nest visit frequency from the dove phase to the sparrowhawk phase). P-values have been adjusted with the Tukey method.

[c] Negative contrasts indicate that urban birds responded less strongly to the sparrowhawk than rural birds, i.e. the difference between the numbers of nest visits in the dove and sparrowhawk phases was smaller for urban than for rural birds.

5.3.4. Correlation between responses to humans and sparrowhawk

Across all birds, responses to humans did not significantly correlate with responses to sparrowhawk either in the case of return latencies ($b = 0.13 \pm 0.14$, $t = 0.90$, $P = 0.378$, $N = 55$) or the numbers of nest visits ($b = 0.04 \pm 0.11$, $t = 0.41$, $P = 0.687$, $N = 55$). We also did not find any significant correlation between responses to humans and responses to sparrowhawk within any of the sites (Table 5.4) and the slopes of this correlation did not differ significantly between urban and forest sites for either dependent variable (Table 5.4, Figure 5.6). Trapped birds tended to return later and visited their nests less frequently than non-trapped birds.

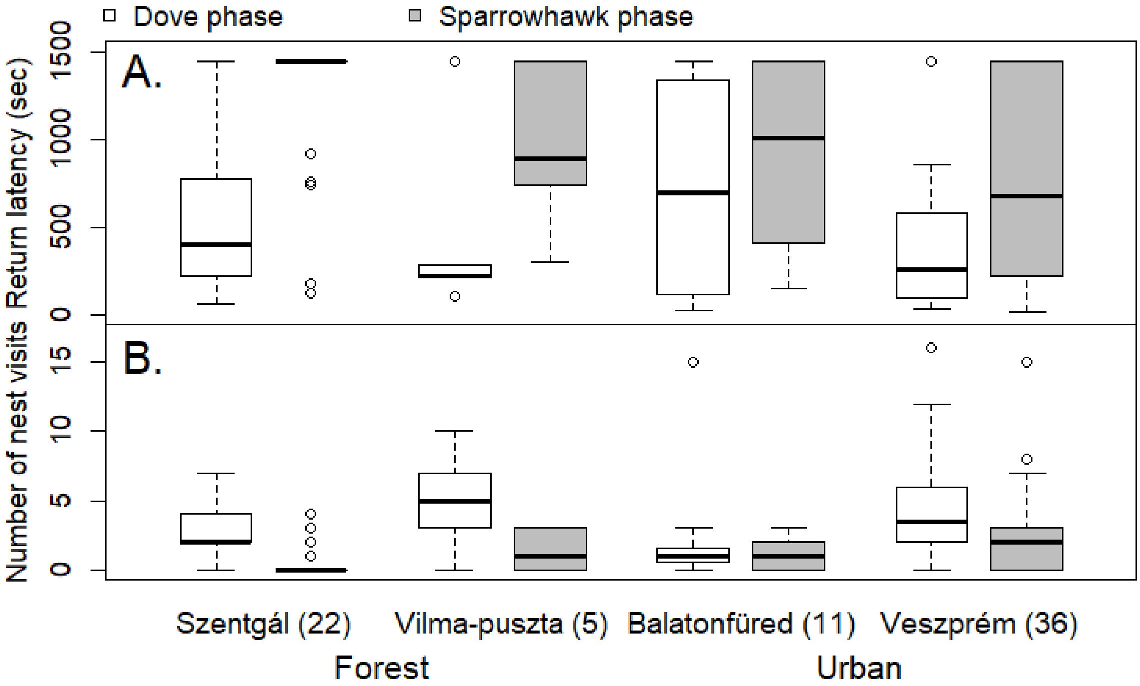

Figure 5.5. *Return latencies (A) and number of nest visits (B) in the sparrowhawk test at the 4 sites. Sample sizes for each site (number of individual birds) are provided in brackets. Boxplots show the median and the upper and lower quartiles, with the whiskers representing data within the 1.5 × interquartile range.*

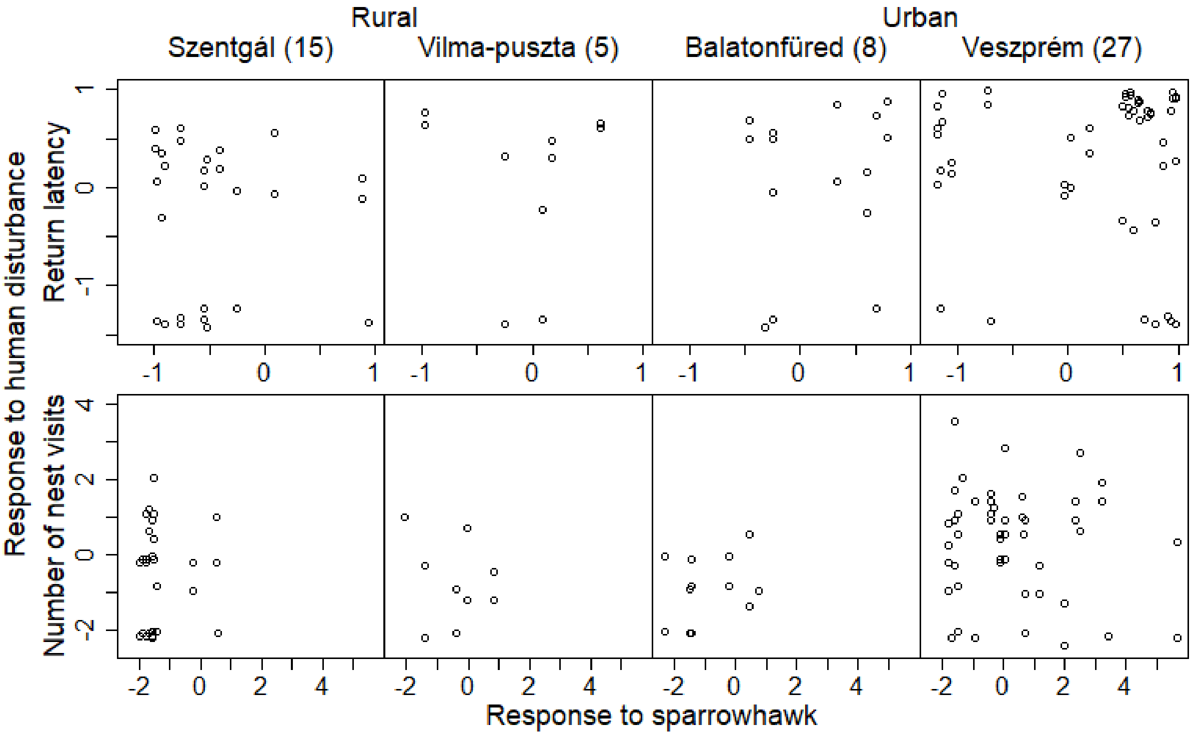

Figure 5.6. *Correlations between responses to humans and responses to sparrowhawk at the 4 sites. Both variables are expressed as residual values, controlling for pre-test behavior (see text for explanation).*

5.4. Discussion

We found that urban great tits were more risk-taking towards humans than great tits from forests were, but birds from neither habitat differentiated between familiar hostile and unfamiliar persons. Furthermore, great tits from forests tended to show stronger avoidance responses towards a sparrowhawk than urban great tits did, but there was no correlation between the birds' response to humans and their response to sparrowhawk either in the entire sample or within any of the study sites.

Table 5.4. *Parameter estimates and random effects of the final models with only significant and marginally non-significant variables, regression slopes from models with behavior in the human disturbance test as dependent variable and behavior in the sparrowhawk test as explanatory variable (testing the relationship between responses to humans and responses to sparrowhawk by great tits), and urban-rural differences (linear contrasts) of these regression slopes (sample size: 55 individuals from 36 pairs). Positive contrasts indicate a more positive slope (i.e. either a stronger positive or a weaker negative correlation) in urban than in rural habitats.*

A) Return latencies

Fixed effects	**Estimate ± *SE***	***df***	***t***	***P***
Response to sparrowhawk	-0.073 ± 0.309	15	-0.24	0.816
Site – Szentgál	-0.293 ± 0.240	32	-1.22	0.231
Site – Balatonfüred	0.041 ± 0.268	32	0.15	0.881
Site – Veszprém	0.353 ± 0.156	32	2.27	0.030
Site – Vilmapuszta	0.344 ± 0.345	32	1.00	0.326
Trapping status – Trapped	-0.439 ± 0.209	15	-2.10	0.053
Response to sparrowhawk:Site – Szentgál	0.426 ± 0.608	15	0.70	0.494
Response to sparrowhawk:Site – Veszprém	0.123 ± 0.356	15	0.35	0.735
Response to sparrowhawk:Site – Vilmapuszta	0.045 ± 0.672	15	0.07	0.948
Random effects	***SD***			
Nest ID	***<0.001***			
Bird ID in Nest ID	0.565			
Residual variance	0.613			
Regression slopes				
Site	**Slope ± *SE***	**95% Confidence interval**		
Szentgál	-0.073 ± 0.309	-0.736 – 0.590		
Balatonfüred	0.353 ± 0.523	-0.768 – 1.474		
Veszprém	0.050 ± 0.180	-0.336 – 0.435		
Vilma-puszta	-0.029 ± 0.598	-1.310 – 1.253		
Contrast of slopes: urban vs rural	**Contrast ± *SE***		***t***	***P***
	0.252± 0.435		0.58	0.571

B) Number of nest visits

Fixed effects	**Estimate ± *SE***	***df***	***t***	***P***
Response to sparrowhawk	-0.105 ± 0.364	15	-0.29	0.776
Site – Szentgál	-0.491 ± 0.556	32	-0.88	0.384
Site – Balatonfüred	-0.452 ± 0.554	32	-0.82	0.420
Site – Veszprém	0.564 ± 0.247	32	2.28	0.029
Site – Vilmapuszta	-0.162 ± 0.641	32	-0.25	0.802
Trapping status – Trapped	-0.922 ± 0.340	15	-2.71	0.016
Response to sparrowhawk:Site – Szentgál	0.424 ± 0.542	15	0.78	0.447
Response to sparrowhawk:Site – Veszprém	0.051 ± 0.385	15	0.13	0.895
Response to sparrowhawk:Site – Vilmapuszta	-0.150 ± 0.617	15	-0.24	0.811
Random effects	***SD***			
Nest ID	<0.001			
Bird ID in Nest ID	0.924			
Residual variance	0.950			
Regression slopes				
Site	**Slope ± *SE***	**95% Confidence interval**		
Szentgál	-0.105 ± 0.364	-0.886 to 0.675		
Balatonfüred	0.318 ± 0.400	-0.540 to 1.177		
Veszprém	-0.054 ± 0.121	-0.313 to 0.206		
Vilma-puszta	-0.255 ± 0.496	-1.319 to 0.808		
Contrast of slopes: urban vs rural	**Contrast ± *SE***		***t***	***P***
	0.313 ± 0.370		0.84	0.412

5.4.1. *Responses to human disturbance*

Urban great tits in our study were less fearful from humans, in line with the numerous studies showing similar habitat differences (Samia et al. 2015). Personality-dependent habitat selection may be an important driver of this difference, as a recent study on great tits found that the distribution of individuals in an urban-suburban area was explained by their boldness towards humans, but the birds did not flexibly adjust their avoidance behavior to the level of urbanization (Sprau and Dingemanse 2017). Nevertheless, we cannot exclude the possibility that habituation or other forms of behavioral plasticity play a major role in the reduction of fear responses in urban great tits compared to conspecifics living in forests. One aspect of our results that supports that great tits do respond flexibly to changes in the level of human disturbance is that trapped birds were more fearful of humans than non-trapped birds (Supplementary Tables S1B & S1D), fitting well with an experimental study in which we found that trapping made great tits more vigilant (Seress et al. 2017). This result in great tits corroborates similar findings on other species that even a brief experience with a hostile human can sensitize animals to subsequent human disturbance (Levey et al. 2009; Marzluff et al. 2010; Vincze et al. 2015). In a similar way, encounters with non-hostile people may facilitate habituation, especially in urban habitats (Vincze et al. 2016).

A further factor that may contribute to the higher risk taking of urban great tits is reduced food availability. Caterpillars, the most important component of great tit nestlings' diet, are much scarcer in urban habitats (Seress et al. 2018), which may constrain the parent birds' behavior upon human disturbance because a respite of chick-feeding might jeopardize the nestlings' survival whereas in forest habitats, where food is more abundant, birds can afford being more risk-aversive. The idea is supported by studies that showed that animals with more abundant food sources tend to take less risk towards humans (Beale and Monaghan 2004a). On the other hand, urban broods in our great tit populations are smaller (in the present study: 3 to 11 nestlings, mean ± *SD* = 7.1 ± 2.2), than forest broods (8 to 13 nestlings, mean ± *SD* = 11.2 ± 1.4), likely also due to reduced food availability (Seress et al. 2018). Small brood size reduces brood value and thereby the parents' motivation to take risks for their chicks (Rytkönen 2002), and also the amount of food required by the nestlings. We controlled for this confounding effect of number of nestlings by including it as a fixed effect in our models.

5.4.2. Responses to hostile versus unfamiliar humans

We found that whether a person was familiar and previously hostile or unfamiliar had very little if any effect on the birds' behavior in the human disturbance test. We only found a marginally non-significant difference in the second phase which might indicate that the birds distinguished between the 2 persons. However, not only was this difference in an unexpected direction, i.e. return latencies tended to be shorter in response to the hostile familiar persons (Table A5.2, Figure A5.3)., but also it was only present in the second phase, and even there it was weak and not statistically significant after P-values were adjusted for multiple comparisons; therefore we conservatively conclude that our birds did not respond differently to the 2 persons.

The lack of differentiation between the familiar and unfamiliar person indicates that great tits either did not recognize the people, or perceived them as equally threatening. Although the ability to recognize individual humans is often associated with particularly intelligent species such as corvids (Marzluff et al. 2010; Lee et al. 2011), it has also been demonstrated in other birds like passerines and pigeons (Levey et al. 2009; Belguermi et al. 2011; Vincze et al. 2015). Great tits often perform well in learning and problem-solving tasks (Sasvári 1979; Preiszner et al. 2017), thus they are likely to have the cognitive capacity for individual recognition of humans. Instead, we suggest that differentiating between humans might have little ecological relevance for both urban and forest great tits, for two reasons. First, recognizing individual humans may be the most relevant in habitats with low but non-negligible human population density (such as farmlands) where repeated encounters with the same individual humans are likely (Vincze et al. 2015). In forest habitats, encounters with humans are very uncommon, whereas in cities, only few of the many people may be encountered repeatedly, at least in public areas like our study sites. Second, as great tits are perceived as pleasant birds by the public, hostility towards them is probably rare in both habitat types. Some species where the ability to differentiate between hostile and non-hostile humans was demonstrated, such as pigeons (Belguermi et al. 2011) and house sparrows (Vincze et al. 2015), have long evolutionary history with humans who have often persecuted them as pests, thus recognizing hostile people is beneficial for them. A third possibility is that, despite the regular nest-checks, the birds did not sensitize to the person who checked the nest and trapped the birds, since all "attacks" on the nest and the parent birds were non-fatal. However, other studies suggest that birds usually perceive the people who check nests as dangerous, as in these studies repeated nest-checking by itself was enough for the birds to recognize and respond to individual humans as potentially threatening (Levey et al. 2009; Lee et al. 2011). Also, in our study, trapping status had significant effect on the response to humans (Table 5.1) but this effect was no different in the familiar and unfamiliar human phases (Table A5.1 C-D). This result indicates that trapped birds sensitized to humans in general rather than specifically to the familiar hostile person.

5.4.3. Responses to sparrowhawk

The finding that both urban and forest birds increased their return latency and decreased their number of nest visits in the sparrowhawk phase compared to the dove phase indicates that our treatments were successful: the birds reacted to the sparrowhawk mount as if it was a predator. Although the order of stimuli in this experiment was fixed (the dove always preceded the sparrowhawk), we think it is unlikely that the difference between the responses to the two stimuli was due to an order effect, for two reasons. First, if there was an order effect, i.e. that birds become more fearful or less motivated to feed during the second stimulus than the first, we would have found a similar pattern in the human disturbance test as well, but instead we found no difference between the responses to the first and second persons. Second, we often heard great tit alarm calls during the sparrowhawk phase (in 27 out of 43 tests) but extremely rarely in the dove phase (in 3 out of 43 tests), indicating a specific anti-predatory behavior towards the sparrowhawk mount.

Urban birds tended to show a weaker response to sparrowhawk, i.e. they did not increase their return latency and reduce their number of nest visits compared to the dove phase to the same extent as forest birds did. This difference was specifically due to the birds' response to the sparrowhawk, because the results did not change qualitatively when we statistically controlled for variation in baseline behaviors (i.e. with no mount present), ; and return latency and number of nest visits in the dove phase were not significantly different between habitats, but return latencies in the sparrowhawk phase were (Table A5.3) The higher risk taking of urban birds might be explained by sparrowhawk attacks being less frequent in cities. For example, some censuses indicate that raptors like sparrowhawks are less common in urban habitats (Møller and Ibáñez-Álamo 2012), possibly because they are more sensitive to human disturbance than smaller prey species (Møller 2012). Furthermore, even predators that are abundant can pose a lower level of threat to some prey species in urban habitats, for example by shifting their diet in cities, preferring easier and/or more abundant prey (Rodewald et al. 2011a). Although we do not have data on great tit predation rates by sparrowhawks at our study sites, our earlier research indirectly suggests that urban sparrowhawks in our area might preferentially hunt for house sparrows (Bókony et al. 2012, Seress et al. 2011).

Alternatively, it is possible that the weaker avoidance response to sparrowhawk is due to a human-mediated spillover effect, i.e. that urban birds reduced their fear from humans, and thus their fear from non-human predators also decreased (Geffroy et al. 2015). We would expect such effect if responses to humans and to non-human predators are part of a behavioral syndrome. This possibility is discussed next.

5.4.4. Correlation between responses to humans and sparrowhawk

The general risk taking hypothesis predicts that responses to humans and to non-human predators are driven by the same proximate mechanisms, and therefore should be correlated not only in the total sample but also within habitats. This is not supported by our results: although urban birds were on average bolder than forest birds both towards sparrowhawks and towards humans, the two behaviors were not correlated significantly with each other either in our total sample or within any of the 4 sites. This indicates that fear of humans and fear ofsparrowhawks are likely to have decreased in urban great tits for different reasons: the former because tolerance of human disturbance is necessary for survival and reproduction in urban habitats, and the latter because sparrowhawk attacks are less common in cities. The fact that trapping status was a significant confounding variable in the human disturbance test (Tables 5.1 & 5.2) but not in the sparrowhawk test (Table 5.3) further supports the idea that birds adjusted their boldness towards humans based on their earlier experiences with humans, but this did not influence their response to sparrowhawk. These findings fit well with the threat-specific predator-discrimination abilities of great tits, which react with distinct alarm calls and different behaviors to snakes and avian nest predators (Suzuki 2011; Suzuki 2012), and mob faster-moving predators like sparrowhawks from greater distances than slower predators like owls (Curio et al. 1983). There are several reasons why responses to humans and sparrowhawks may be distinct: humans are relatively slow-moving, terrestrial and seldom hostile with great tits in our study sites, and when they are, they are primarily threatening towards the nests (i.e. nest checks), whereas sparrowhawks are fast, aerial and specialized in hunting small passerines such as great tits, thus primarily threaten adult birds. Differential responses to such threats may be due to learning; for example, rabbits can learn not to fear humans or cats depending on early-life experiences (Pongrácz et al. 2001).

In contrast to our results, two earlier studies found that non-urbanbirds (song sparrows *Melospiza melodia* and burrowing owls *Athene cunicularia*, respectively) with shorter flight initiation distances from humans showed more intense mobbing behavior towards non-human predators, while the same correlation was absent in urban birds (Myers and Hyman 2016; Carrete and Tella 2017). These two studies notably differ from ours in that they assessed responses to humans through avoidance behavior (flight initiation distances) and responses to non-human predators through aggression (mobbing), whereas we assessed both behaviors through avoidance (delaying and reducing the frequency of returns to the nest box where humans/sparrowhawk appeared). Interestingly, both earlier studies found that behaviors within the same domain (i.e. avoidance or aggression) remained correlated even in urban habitats: there was a habitat-independent correlation between avoidance of humans and avoidance of novel objects (Carrete and Tella 2017), as well as between aggression towards predators and aggression towards conspecifics (Myers and Hyman 2016). Despite focusing on a single domain, however, we found no risk-taking syndrome in great tits. In line with this, a recent study on great tits did not find correlation between object neophobia and predator avoidance, suggesting that the various domains of risk taking do not covary in this species (Davidson et al. 2018). Taken together, these findings suggest that detecting the existence or breakdown of behavioral syndromes might depend on the way behaviors are quantified.

5.4.5. Conclusions

Risk taking towards humans and towards non-human predators are two forms of behavior that are often considered to be correlated. We found that although urban great tits are bolder both towards humans and towards sparrowhawks than forest-dwelling great tits, the two behaviors do not correlate with each other either in our total sample or within habitats, which suggests that the habitat-specific changes in risk-taking behavior of great tits are threat-specific rather than driven by a general syndrome. These results have several implications for the methodology of investigating anti-predator behavior. First, behavior towards humans may not necessarily be a reliable indicator of overall anti-predator behavior (Seress and Liker 2015). Several studies treat the two as equivalents, using responses to humans as an estimate of fear from predators in general (Møller 2012; Møller and Ibáñez-Álamo 2012; Møller et al. 2013; Jiang and Møller 2017). Our results suggest that responses to humans and to non-human predators do not necessary covary, thus we need to be careful with this kind of interpretation. Second, our results show that measuring the same behavior on different levels (i.e. populations versus individuals) can lead to different conclusions. If we compare the mean behavior between habitats, we may come to the conclusion that responses to humans and responses to sparrowhawk are strongly related to each other, as urban birds were more risk-taking towards both stimuli. However, looking at correlations between the two responses on the individual level can lead to the opposite conclusion, i.e. that there is no relationship between responses to humans and responses to sparrowhawk. Because of this, it is important to look at behavioral variation on both levels. Third, the contrast between our results and other recent studies addressing the relationship between responses to humans and to non-human predators (Myers and Hyman 2016; Carrete and Tella 2017) suggest that estimating the same trait (e.g. risk taking) from different forms of behavior (e.g. aggression and avoidance) might yield different results. Therefore, comprehensive studies investigating several behavioral domains at the same time along the urbanization gradient will be important for furthering our understanding of urban adaptations.

Finally, our results also have some implications for wildlife conservation. It has been suggested that in habitats with high anthropogenic disturbance, animals are more susceptible to predation due to the human-mediated spillover effect (Geffroy et al. 2015). However, our results support threat-specific rather than general risk-taking responses to urbanization, suggesting that at least some species like the great tit may not suffer increased mortality from predation due to tolerance of humans. On the other hand, our birds did not adjust their behavior to the threat based on previous experience with individual people, suggesting that species historically not exposed to persecution or other selection pressures for the discrimination of persons might be vulnerable to human hostility even after a relatively long evolutionary past of co-existing with humans. Exploring how widespread threat-specific responses are across species, and what cognitive, ecological and evolutionary processes lead to them, is an interesting direction of future research.

CHAPTER 6:

URBANIZATION'S EFFECTS ON PREDATION OF BIRD NESTS: A META-ANALYSIS[5]

6.1.Introduction

Urbanization, i.e. the expansion and development of cities, creates novel, and often challenging, environments for wild animals. Compared to natural areas, urban habitats are characterized by many altered environmental factors such as elevated levels of chemical, noise and light pollution, severely transformed landscapes or various disturbances resulting from the increased human population (Marzluff et al. 2001a; Sol et al. 2013; Sprau et al. 2016). These altered environmental factors profoundly impact ecological factors that essentially affect population dynamics and persistence, such as food availability and predation pressure (Seress and Liker 2015). As a consequence, interspecific interactions such as predator-prey relationships can differ qualitatively between urban and non-urban habitats (Faeth et al. 2005; Chace and Walsh 2006; Fischer et al. 2012).

Although avian species are frequently used model organisms in urban ecological studies on predation, it is unclear whether and how urbanization affects predation on birds and their nests. Different mechanisms have been postulated that predict either increased or decreased rates of predation in cities (Chamberlain et al. 2009). While some hypotheses suggest that prey species thrive in cities because those habitats are 'predator-safe zones' (Gering and Blair 1999; Ryder et al. 2010; Møller 2012), others predict an opposite relationship, with predators thriving in cities and imposing increased predation pressure on their prey (Jokimäki and Huhta 2000; Haskell et al. 2001). Notably, the suggested mechanisms are non-exclusive, and thus any difference in predation rates between urban and rural habitats, or lack of it, may also be a net result of their joint effects. For example, larger species are often less tolerant towards high human density; as predators are usually larger than their prey, they are expected to be present in lower abundances in cities compared to natural habitats, resulting in lower predation rates (Møller 2012). However, many opportunistic, medium-sized predator species, such as crows (*Corvus sp.*) (Marzluff and Neatherlin 2006; Kövér et al. 2015), magpies (*Pica pica*) (Jerzak

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[5] This chapter is a modified version of the research article „Ernő Vincze, Gábor Seress, Malgorzata Lagisz, Shinichi Nakagawa, Niels J. Dingemanse & Philipp Sprau (2017): Does urbanization affect predation of bird nests? A meta-analysis. Frontiers in Ecology and Evolution 5:29"

1997), or raccoons (*Procyon lotor*) (Haskell et al. 2001; Prange and Gehrt 2004), are known to reach higher densities in urban compared to rural habitats. Such patterns may suggest that these species also pose higher predation pressures on their prey species in urban habitats. Similarly, domesticated predators, particularly cats (*Felis silvestris catus*), are often found in extremely high abundances in urban and suburban areas (Sims et al. 2008), and increase the risk of predation for avian species (Baker et al. 2008; Stracey 2011; Balogh et al. 2011). Other authors, by contrast, suggest that, despite this high abundance of certain predator species, urban predation rates can still be low if urban prey populations are also relatively large, which may explain the ‘urban predation paradox’ (Rodewald et al. 2011a; Fischer et al. 2012).

Environmental characteristics of urban habitats, such as noise (Slabbekoorn and Halfwerk 2009), light (Navara and Nelson 2007) and vegetation (Chace and Walsh 2006) can also affect predation rates, again either positively or negatively. For example, high noise levels in cities may increase the difficulty for prey animals to detect predation risk and to respond to it, resulting in increased predation rates (Templeton et al. 2016). Urban noise can, by contrast, also disturb predators and make it more difficult for them to detect their prey, thus resulting in decreased predation rates (Francis et al. 2009), For example, noise is known to influence begging calls of nestlings (Leonard and Horn 2008), and it might be possible that it conceals the vocalizing chicks from predators. Similarly, artificial lighting (which is abundant in cities) can make prey more conspicuous to predators, increasing predation rates (Clarke 1983), but also make it easier for prey to detect predators (Gorenzel and Salmon 1995). Furthermore, vegetation is more fragmented in urban habitats, and fragmentation can increase predation risk (Hartley and Hunter 1998), possibly because there is less shelter for prey animals.

Weaker anti-predator responses of urban animals (compared to non-urban conspecifics) have also been described as indirect evidence for decreased predation risk in cities (Møller and Ibáñez-Álamo 2012). However, apart from a handful of experiments with predator dummies (Seress et al. 2011; Bonnington et al. 2013) or playbacks of alarm calls (Myers and Hyman 2016), the majority of empirical studies comparing anti-predator behavior of urban and rural populations have been conducted using humans as potential predators (reviewed by Samia et al., 2015). While humans might be perceived as potential predators, they usually do not represent a direct predation threat (Beale and Monaghan 2004b). Therefore, these results are difficult to generalize to non-human predators. In fact, tolerance of humans can also lead to decreased vigilance in prey, which can lead to higher predation rates in urban areas (Geffroy et al. 2015).

Studies investigating mechanisms postulated above have used a diverse array of methods. Some studies compare the diet composition of urban and rural predators, e.g., using remains found in pellets of birds of prey (e.g., Brack et al., 1985; Kristan et al., 2004; Lesiński et al., 2009). However, while pellet analysis can be informative regarding the relative predation pressure on various prey species, it tells very little about the overall predation pressure. Another approach is the direct monitoring of prey mortality. Studies comparing post-fledging and adult mortality between urban and non-urban habitats are uncommon, because population censuses and capture-recapture methods (Chiron and Julliard 2007; Brown and Graham 2015) might estimate survival inaccurately, or because tracing individual prey animals (e.g., by radio-telemetry; Ausprey and Rodewald, 2011; Balogh et al., 2011; McCleery et al., 2008; Shipley et al., 2013) is often costly and based on small sample sizes. Bird nests, in contrast, are immobile, easy to monitor, and are often preyed upon by various predator species. Thus, natural bird nests, as well as artificial nests baited with real or fake eggs, are most often used as study system when comparing predation rates between differently urbanized habitats. However, a number of factors may increase heterogeneity in effects reported in the literature, hindering interpretation and generalization of results, such as differences in characteristics between artificial and natural nests (Moore and Robinson 2004; Robinson et al. 2005), nesting characteristics specific of the study species (e.g., nest height from the ground, nest openness), and inconsistent, study-specific definitions of urbanization (Marzluff et al. 2001b).

In this chapter, we investigate how predation rates on bird nests change with habitat urbanization by conducting a formal meta-analysis. To our knowledge, this is the first formal meta-analysis that attempts to quantitatively synthetize published results. Furthermore, we also conducted meta-regressions (meta-analyses with additional explanatory variables, henceforth referred to as “moderators”), to explore whether variation in effect size between studies can be explained by differences in study design (using natural vs. artificial nests), bird species, or definitions of predation rate or urbanization.

6.2.Methods

6.2.1. Literature screening and data collection

We followed the PRISMA protocol for collecting data from the published literature (Moher et al. 2009; Nakagawa and Poulin 2012). We first performed literature searches using the online search engines Scopus (http://www.scopus.com/) and Web of Science (http://wokinfo.com/) with the following keyword string: “*nest* AND (*urban* OR anthropogenic OR rural) AND* *predat**”. We then screened the titles and abstracts of the papers found by the search, and decided whether the following criteria were met:

- The abstract indicated that study was conducted on bird nests; either by monitoring natural bird populations, or by performing experimental studies on artificial nests baited with real or fake eggs.
- The abstract indicated that the survival (or mortality) rates of these nests were reported in the main text as a function of an urbanization gradient.

I screened all the abstracts found by Scopus, while another observer (Gábor Seress) screened all the abstracts found by searching the Web of Science (WoS), and coded whether the papers met the selection criteria or not. Papers that were found by both search engines were scored by both observers and used for testing between-observer repeatability (see Table A6.1). We also performed backward searches, i.e. screened reference lists of relevant papers and reviews, and visited author websites, to find additional eligible papers that might have been missed during the systematic database searches. We did not limit our search to English-language papers, but also included papers written in Spanish, French, German, Russian or Polish; however, these non-English papers were relatively few (4% of the literature we screened).

Papers considered to meet the selection criteria by at least 1 observer were taken forward for full-text screening. Each paper was screened by a single person. During full-text screening we excluded the papers that:

- did not define an urbanization gradient (i.e. because all studied sites had the same level of urbanization, or because the information was not provided);
- addressed other forms of anthropogenic disturbance (i.e. fragmentation of natural or semi-natural habitats, agricultural practices) without using any urban study sites;
- did not report any nest survival (or mortality) data, only presence/absence of species, adult survival or individual offspring survival;
- had overlapping data with another paper (i.e. when two papers tested different hypotheses using the same dataset). In these cases we included the paper which contained the most information (i.e. reported more complete data or used a larger data set);
- did not report their nest survival data in relation to urbanization, despite conducting the study in differently urbanized habitats;

- reported the data in a format that did not allow extraction of effect sizes (e.g., multivariate regressions, mixed-effects models, daily survival rates from logistic exposure models – see further justification in section Data extraction).

In the latter two cases, we contacted the original authors provided that their e-mail addresses were available. We got feedback from 19 out of 28 contacted authors. For 4 studies, we obtained raw data from the authors from which we managed to extract effect sizes ourselves; we also included these papers in the analysis.

6.2.2. Scoring urbanization

Studies varied widely in methods used to quantify urbanization. To make studies comparable, 2 observers (Gábor Seress and I) independently scored the level of urbanization of the sites (i.e. the areas where the nests were located, representing one level of urbanization) for each study, based on the information available from the papers or received from the authors, on a 5-level urbanization scale (using a modified version of the scale proposed by Marzluff et al. 2001a):

1. Wildland / natural area: Interior of a large (> 200 ha) forest or meadow, with little anthropogenic effects.
2. Rural area: Landscape dominated by anthropogenic effects, such as agriculture (pasture, crop field, orchard, farmland), or very intensive forestry (clear-cuts), with little housing (< 2.5 / ha); or a small forest patch (< 200 ha) / forest edge within these types of landscapes.
3. Suburban edge / exurban area: Landscape in the proximity of urban or developed industrial areas, with a low housing density (< 2.5 / ha) or a low proportion of built / developed surface (< 20%, or > 80% vegetation), e.g., brownfields, golf courses, areas with detached houses; or a small forest patch (< 200 ha) / forest edge within a suburban matrix.
4. Suburban area: Landscape with medium housing density (2.5 – 10 / ha) or medium proportion of built / developed surface (20 – 50%; or 50 – 80% vegetation), e.g., most urban parks, residential areas with single-family houses, lawns and gardens, university campuses.
5. Urban area: Landscape with high housing density (> 10 / ha, 1000 / km^2) or high proportion of built / developed surface (> 50%; or < 50% vegetation), e.g., residential areas with multi-story buildings and blocks of flat, commercial, service and industrial buildings.

Information on numbers of sites scored by the 2 observers, and on between-observer repeatability, is provided in Table A6.2. Sites that got different scores from the 2 observers were assigned 1 of the 5 scores via subsequent discussion. In most studies (N = 40; 78%), the order of the study sites based on these urbanization scores matched the order indicated by the original authors. However, for some papers (N = 11), sites that represented different urbanization levels according to the authors were given equal scores by us. To test whether this qualitatively changes the results, we run sensitivity analyses (see below).

6.2.3. Data extraction

We used correlation coefficients between nest survival (i.e. the probability of nests not failing) and urbanization as our effect size. We decided to use this estimate rather than odds ratio (*OR*) because this way we could include studies that quantified nest mortality in more than two urbanization levels. We calculated these correlation coefficients from the numbers of surviving and failed nests at each study site unless already provided in the paper. The numbers of surviving and failed nests were obtained in several ways:

i) the exact numbers of surviving and failed nests in an experiment were directly reported (N = 22) or given to us by the original authors (N = 4);

ii) the numbers could be calculated by multiplying the reported percentage of survived nests by sample sizes (N = 20);

iii) if the survival rates were reported in figures as column diagrams (N = 3), we measured the height of the columns and calculated the number of surviving and failed nests from these;

iv) 1 paper reported daily nest survival rates calculated by Mayfield's method (Mayfield 1961; Mayfield 1975) along with the numbers of exposure days; for this paper we calculated the number of failed nests by multiplying daily predation rate by the number of exposure days. Other papers that reported daily nest survival rates (N = 7, Table A6.3) were excluded, as we did not find a reliable way to back-calculate the number of survived and failed nests.

There was a single paper that reported only a correlation coefficient (Lumpkin et al. 2012), which we used as our effect size. For all other papers we coded each nest as failed (0) or survived (1), ranked urbanization of the site in which the nest is found on the 5-level ordinal scale described in 6.2.2, and ran a Spearman rank correlation between these two variables for each study. We used the Fisher's Z-transformed correlation (Z*r*) value as our effect size (see Statistical analyses below for more explanation for this choice). We excluded studies where only test statistics from regression models other than correlation tests were available for which we did not obtain data from the authors (N = 18, Table A6.3). We excluded these studies because the conversion of multivariate regression estimates to correlation coefficients often does not accurately approximate correlation coefficients when calculated from raw data (Aloe 2015). Sampling error variance of each effect size (Fisher's *Zr)* was calculated as the reciprocal of the total number of nests minus 3.

Some papers (N = 16 natural nest studies and N = 20 artificial nest studies) distinguished between predation and other forms of nest failure (e.g., abandonment, weather destroying the nest, vandalism by humans). Since we were primarily interested in predation, whenever it was possible, we omitted nests that died due to other causes than predation, and used only nests that survived and nests that failed due to predation. For papers that did not distinguish between sources of nest failure (N = 15 studies, all on natural nests), we simply used numbers of survived and failed nests to calculate effect sizes, regardless of the actual source of nest failure. Similarly, partially predated nests (i.e. where some eggs or offspring disappeared, but at least one of them survived) were considered as predated in some studies (N = 19) and as survived in others (N = 28). Some studies were conducted on nests with only 1 egg (N = 4), thus partial predation is not meaningful for these; we considered these as a third category. To test whether these two methodological differences affected our effect sizes, we applied the moderator 'source of mortality' as a binary factor to describe whether our effect size was calculated from predation-only mortality or from total mortality, and the moderator 'partial predation', also as a binary factor, to code whether failed nests included the partially predated nests or not.

For studies spanning over multiple years, we extracted separate effect sizes for each year, with 'study year' as a moderator. However, in some papers only pooled data from multiple years were available. In these cases we used the median value of all study years as a measure of 'study year'. We also recorded the following moderators: whether the study reported observational data collected in a natural population (N = 28) versus experimental data using artificial nests (N = 20); the number of eggs per nest (average number for natural nests, exact number for artificial nests); nest position (ground nest or elevated, e.g., on a tree or building); nest height above ground in meters; nest openness (cup nest – a hemispheric, open nest on the ground or a branch; orb nest – a spherical nest closed on top; or cavity nest – one inside a den or a box); the number of days the nest was exposed to predators (the length of the experiment for artificial nest, the length of the nesting cycle, from egg laying until fledging, for natural nests); and, in case of natural nests, the study species. We also recorded the year and journal in which the paper was published.

6.2.4. Statistical analyses

Before conducting analyses, we converted correlation coefficients r (Spearman's r) into a standard normal metric (using Fisher's z transformation), Zr. This was done because r is bounded between -1 and 1, and thus does not follow a normal distribution (Hedges and Olkin 1985). All analyses were performed using the transformed values (Zr), but the results were transformed back to correlations (r) for visual presentations. Correlational effect of $r = 0.1, 0.3$, and 0.5, can be considered as small, medium and large effect sizes, respectively, following Cohen's (1988) tentative benchmarks. Point estimates from statistical models were considered significantly different from zero when their 95% Confidence Intervals (CI) did not overlap zero.

We performed all statistical analyses within R statistical software v3.2.4 (R Core Team 2016), For meta-analysis and meta-regression we used the *metafor* package (Viechtbauer 2010). The phylogenetic tree for the bird species included in the dataset was created by us based on data from the global phylogeny of birds (Jetz et al. 2012) and visualized using the *ape* package (Paradis et al. 2004). We used multilevel meta-analyses, representing a type of linear mixed model (Viechtbauer 2010; Nakagawa and Santos 2012), to control for various sources of non-independence in the data. Non-independence can be present when multiple effect sizes are extracted from the same study, multiple effect sizes are available for the same species, and / or due to phylogenetic relationships among species. To take such non-independences into account, we included random intercepts for study identity, species identity (for natural nests), and phylogeny (for natural nests; using phylogenetic meta-analysis, Hadfield and Nakagawa, 2010; Nakagawa and Santos, 2012) in our models.

6.2.5. Meta-analyses and meta-regressions

We first ran a simple meta-analytical model (an intercept-only model without any moderators) on all available data to examine the overall effect, which tested whether the meta-analytic mean was different from zero. This meta-analytic mean represents the overall relationship between urbanization level and nest predation rate over all data. We quantified total heterogeneity in the dataset by computing I^2 statistic (Higgins et al. 2003), which reflects the percentage of variance that is due to study heterogeneity rather than sampling error (Higgins and Thompson 2002). We also assessed separate meta-analytical models (and quantified heterogeneity) for the two data subsets composed of effect sizes from studies using either artificial or natural nests, respectively. To interpret the difference between the predation rates in differently urbanized habitats, we converted our meta-analytical means from correlation coefficients to odds ratios (Borenstein et al. 2009), and we report both numbers.

We conducted meta-regression analyses to identify variables accounting for heterogeneity across studies. Continuous moderators were standardized prior to the analyses, so that they had a mean of 0 and *SD* of 1. Nest height above ground was log-transformed due to skewedness. We first quantified whether the relationship between urbanization and predation differed on average between the two major study approaches, i.e. artificial versus natural nest studies. To do so, we added nest type (artificial versus natural) as a moderator. Because the data subsets for artificial and natural nests had different combinations of applicable moderators, we then performed separate meta-regression analyses on these two data subsets. We did not construct models with multiple moderators, because the sample sizes of the subsets were inadequate and / or information on key moderators was missing for many data points. For artificial nests we considered the following moderators: nest openness (cup / hole), nest position (elevated / ground / mix), average egg number per nest, study duration, median study year, study publication year, minimum (min) urbanization score of the site gradient (1 / 2 / 3 / 4), maximum (max) urbanization score of the site gradient (3 / 4 / 5). For the natural nests, we considered the following moderators: source of mortality (i.e. whether failures due to other causes than predation were excluded from calculating the effect sizes or not: yes / no), nest openness (cup / hole / orb), nest position (elevated / ground), nest height above ground in meters, average egg number per nest, study duration, median study year, study publication year, minimum urbanization score of the site gradient (1 / 2 / 4), maximum urbanization score of the site gradient (3 / 4 / 5).

6.2.6. Sensitivity analyses and publication bias

As there were some sites within a study that represented different levels according to the authors, but got equal ranks on the 5-level scoring system applied by us, we tested whether our results were sensitive to the way we scored urbanization. In this sensitivity analysis, we ranked all sites within a study on an ordinal scale from the least urbanized to the most urbanized, based on which sites were treated as different urbanization levels in the original papers. Then we calculated effect sizes from these alternative urbanization scores using the same method as describen in 6.2.3, and repeated all analyses with these effect sizes.

We also assessed evidence for publication bias which can affect conclusions of meta-analytic studies when published studies are biased towards significant findings (Rothstein et al. 2005). We assessed the existence of publication bias in three ways. First, we visually assessed funnel plot asymmetry. In a funnel plot, the estimate of effect size in each study is plotted against an estimate of its precision (the inverse of standard error or the square-root of sampling error variance). If studies with low precision that have non-significant results are missing from the data set due to publication bias, the shape of the funnel will be asymmetric. Second, we analyzed funnel plot asymmetry using Egger's regression test (Egger et al. 1997) using the *regtest* function in the *metafor* package (Viechtbauer 2010). Egger's test indicates publication bias when an intercept of standardized residuals regressed on precision is significantly different from zero. Finally, we used trim-and-fill method to identify funnel plot asymmetry arising from publication bias. This method estimates the number of studies potentially absent from a meta-analytic dataset due to the publication bias affecting the most extreme results on one side of the funnel plot.

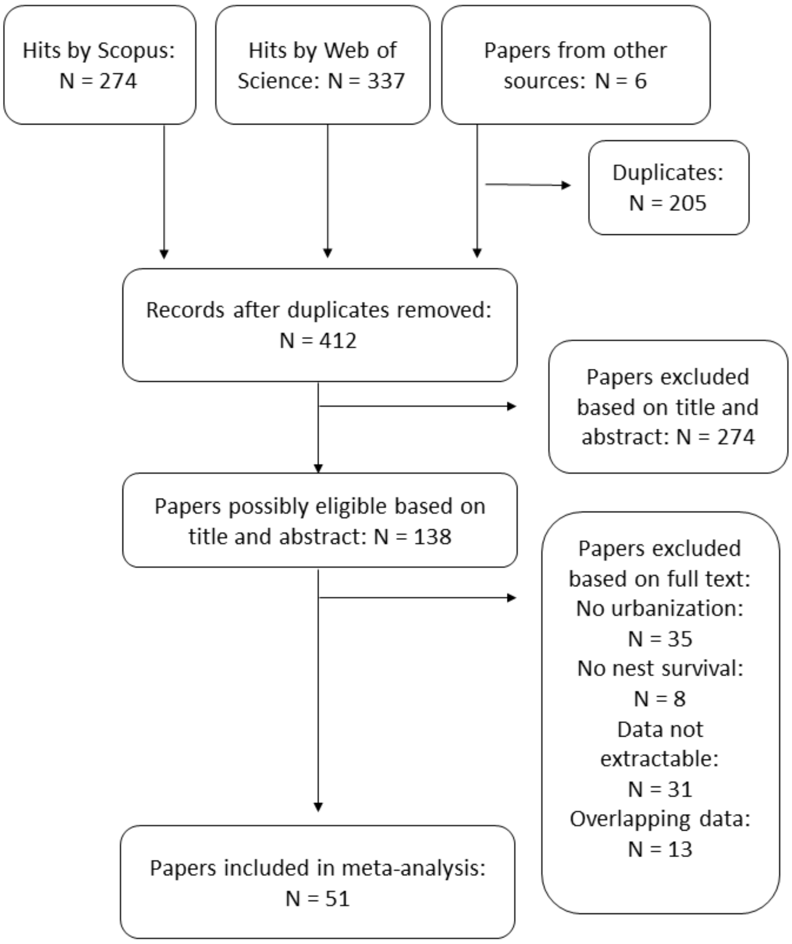

Figure 6.1. *PRISMA diagram showing study search and selection process.*

6.3.Results

6.3.1. General results

We screened the abstracts of 412 papers, 138 of which were taken forward for full-text screening (Figure 6.1). We excluded 87 papers based on our inclusion criteria (fully detailed in Table A6.3). Our final dataset thus comprised 117 effect sizes from 51 papers published between 1985 and 2015 (Table A6.4). The median number of nests monitored within a publication was 104 (mean ± *SD* = 177.6 ± 246.5); only in 8 cases were effect sizes calculated based on sample sizes of more than 500 nests. Almost half of the effect sizes came from studies that scored mortality in natural nests (58, versus 59 effect sizes for studies using artificial nests).

Studies using artificial nests differed from those with natural nests in several aspects of their study design (Table A6.5). First, artificial (versus natural) nests were, on average, followed for much shorter periods of time (mean ± *SD* = 12.2 ± 5.9 versus 41.2 ± 21.1 days). Second, studies using artificial nests were more often performed in less urbanized locations. Third, artificial nests were located on the ground in about half of the studies (28 out of 59 effect sizes), whereas natural nests were usually located at least 2 m above ground level. Fourth, artificial nests were usually open, i.e. cup-shaped (90%; 53 out of 59 effect sizes) and 10% were hole-like (nesting box / cavity). In contrast, natural nests were open in 62% of our data points (36 out of 58 effect sizes), and 34.5% were hole-like. Fifth, failures of artificial nests were always assumed to result from predation (100%), whereas most studies on natural nests reported overall survival rates that did not distinguish between predation and other sources of mortality (66%; 38 out of 58 effect sizes). Finally, all artificial nests were considered as predated when at least 1 egg / offspring died, while in natural nests usually only complete brood loss was counted as a predation event (97%; 56 out of 58 effect sizes). Effect sizes from natural nest observations represented 32 different species from 21 Families within 6 Orders (with 25 species from 16 Families belonging to the Order *Passeriformes*). Most species were represented in our meta-analysis by only 1 study; only data for the House wren *Troglodytes aedon*, European magpie *Pica pica* and Common blackbird *Turdus merula* were available from 2, 3 and 3 studies, respectively (Table A6.4). All continents (except for Antarctica) were represented in the meta-analysis, with most data from North American (46 effect sizes from 23 studies) and European (46 effect sizes from 15 studies) species (Table A6.4).

6.3.2. Meta-analyses and meta-regressions

We found no overall relationship between nest survival and level of urbanization: the meta-analytic mean for the slope between urbanization gradient and nest survival was not distinguishable from, and was centered around, zero (meta-analytical mean (*β*) = -0.003; 95% Confidence Intervals (*CI*) = -0.080 to 0.074; *OR* = 0.99; Figure 6.2, Table A6.6). Effect sizes were, at the same time, highly heterogeneous (I^2 = 92.7%). High heterogeneity suggests effects of moderators, and this finding thereby justified our subsequent meta-regression analyses (Higgins and Thompson 2002).

When meta-analytic means were estimated separately for the subsets of studies using artificial nests and studies using natural nests, we found weak evidence for an effect of urbanization on nest survival for both cases. The meta-analytic mean for artificial nest studies was small and negative, with confidence intervals marginally overlapping with zero, suggesting a decreasing nest survival with increasing urbanization (*β* = -0.118; 95% *CI* = -0.238 to 0.006, *OR* = 0.65; Figure 6.3A; Table A6.7).

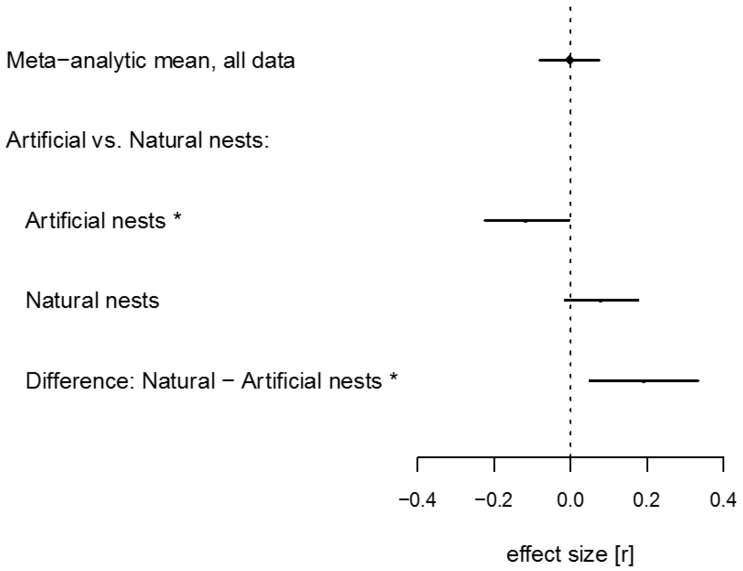

Figure 6.2. *Forest plot representing results of analyses performed on the full data set. The meta-analytic mean indicates overall effect when data from studies using artificial and natural nests are combined. Meta-regression models estimated intercepts independently for studies using artificial and natural nests, respectively, and the difference between overall effect sizes for these two data subsets. Points represent mean estimates from the models, lines represent 95% Confidence Intervals. Positive mean estimates indicate higher survival in more urbanized habitats. Stars indicate estimates that are significantly different from zero (95% Confidence Intervals not crossing zero).*

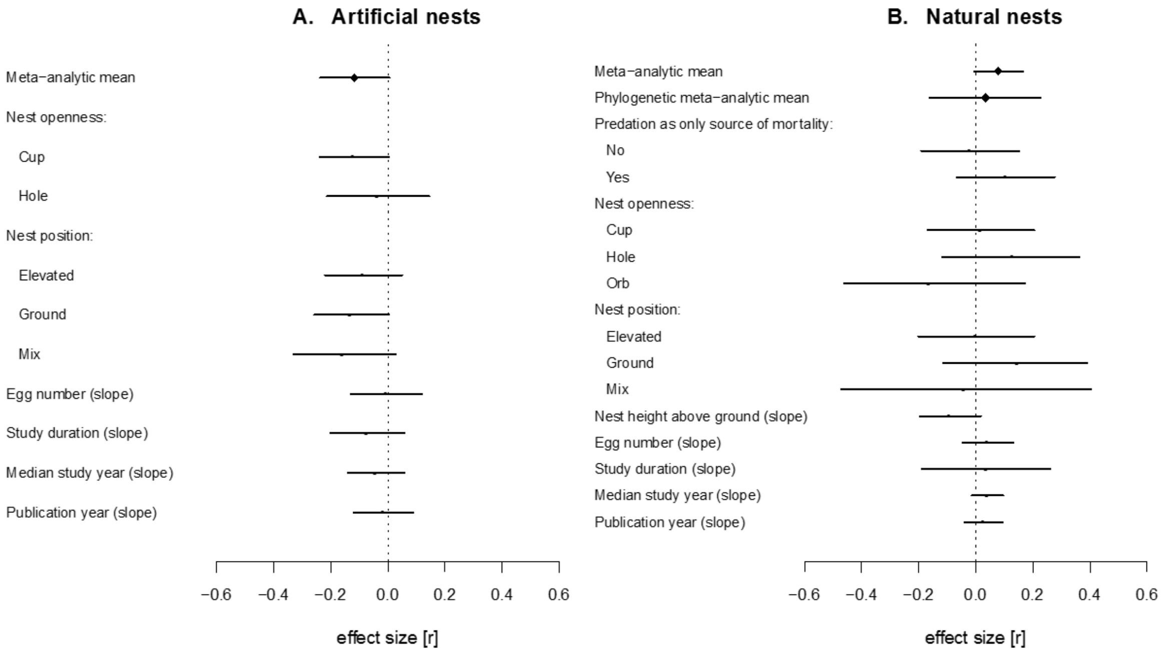

Figure 6.3. *Forest plots of effects size estimates for the studies using artificial nests (A) and natural nests (B). Positive estimate value for meta-analytic mean indicates higher survival in more urbanized habitats. Positive estimate values for moderators can be interpreted as increased likelihood positive effect sizes (higher survival in more urbanized habitats) with increasing values of a continuous moderator, or for a given level of a categorical moderator.*

In contrast, the meta-analytic mean for natural nest studies was small and positive; again, confidence intervals were marginally overlapping zero, suggesting that nest survival increased (instead of decreased, see above) with urbanization (β = 0.079; 95% *CI* = -0.007 to 0.165, *OR* = 1.33). The latter effect was lessened when phylogeny was taken into account (β = 0.034; 95% *CI* = -0.163 to 0.228, Figure 6.3B, Table A6.8) (we note that phylogenetic effects were not applicable for artificial nest studies, as those did not have associated species). Total heterogeneity was above 90% in all meta-analytic models (Table A6.6-8).

When we included nest type (artificial vs. natural nests) as a moderator in the meta-regression model on the full data set, the intercept for studies using artificial nests was significantly different from zero, whereas for studies using natural nests, the confidence intervals around the intercept marginally overlapped with zero (Figure 6.2, Table 6.6). The difference between average effect sizes for artificial and natural nests was small but statistically significant (difference between β artificial and β natural = 0.195; 95% *CI* = 0.050 to 0.332; Figure 6.2; Table A6.6), implying that the slopes of the urbanization-mortality relationship differ between the two nest types. Moderators considered affected the relationship between urbanization and nest predation neither in artificial nest (Figure 6.3A; Table A6.7) nor in natural nest studies (Figure 6.3B; Table A6.8). When we used species identity as a moderator, we found high variation among species (Figure 6.4, Table A6.9); note, however, that most species were represented with only 1 study in the meta-analysis, making further interpretations of this latter result difficult.

6.3.3. Sensitivity analyses and publication bias

All analyses using alternative urbanization scores (based on the quantification of urbanization levels by the original study authors) had results qualitatively identical to these from the main analyses (Tables A6.10-A6.13), indicating that our results are robust to the way urbanization was scored. Two moderators that were close to statistical significance in our original meta-regression models (source of mortality and nest openness) became statistically different from zero in the new models: the difference in survival rates of natural nests between urban and non-urban habitats was smaller when failures other than predation were included in the calculation of effect sizes than when effect sizes were calculated from predation only, and natural cavity nests are predated significantly less in urban than in rural habitats, while natural open nests (both cup- and orb-shaped) show no such habitat difference (Table A6.12).

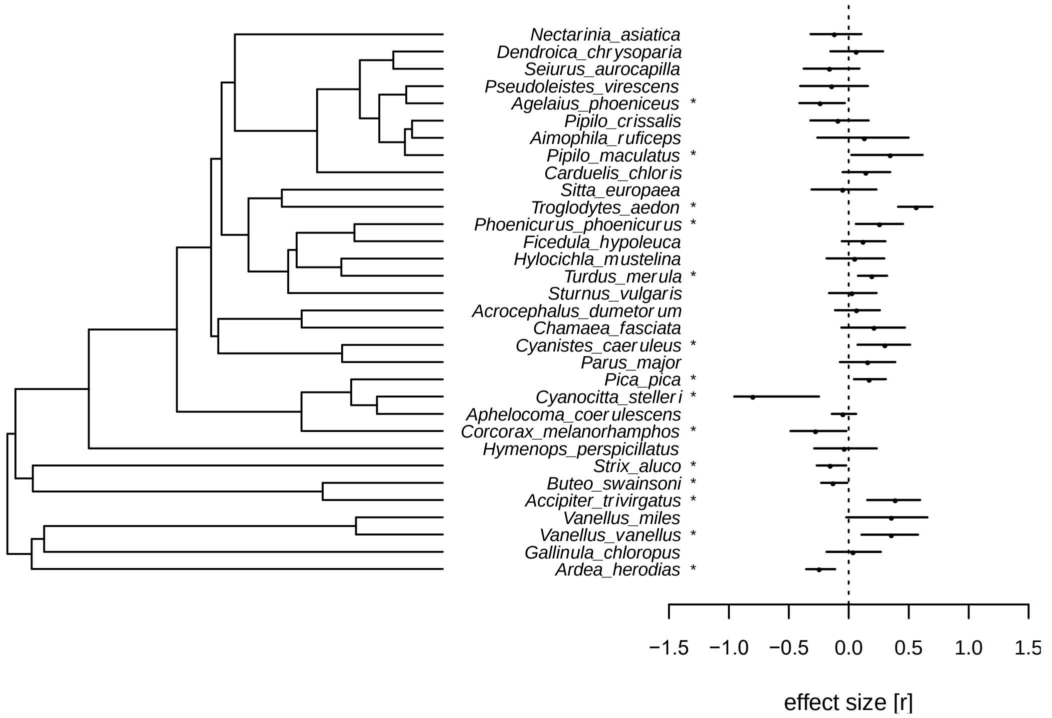

Figure 6.4. *Phylogenetic tree of bird species represented in the studies on natural nests, on the left. Forest plot on the right shows results of analyses performed using species as a moderator in a meta-regression model on this data subset. Points represent mean estimates from the models, lines represent 95% Confidence Intervals. Positive mean estimates indicate higher survival in more urbanized habitats. Stars indicate estimates that are significantly different from zero (95% Confidence Intervals not crossing zero).*

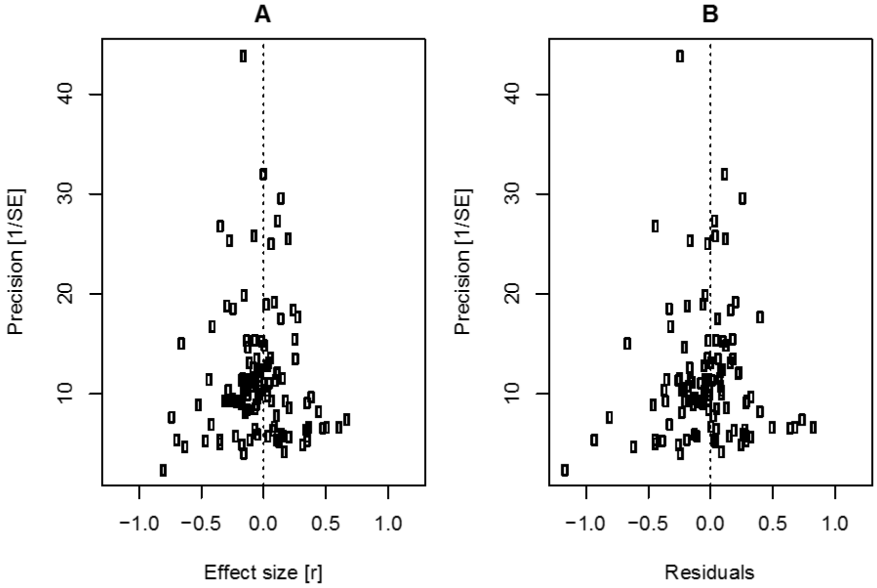

Figure 6.5 *Funnel plots used to estimate publication bias in the data set. (A) Effect size estimates plotted against their precision; (B) Residual effect sizes from the model with nest type (artificial nest / natural nests) used as a moderator. The dashed line indicates zero, i.e. no relationship between nest mortality and urbanization scores.*

We found no evidence for publication bias. Visual inspection of funnel plots and Egger's regression test revealed no indication of funnel shape asymmetry (Figure 6.5; $t_{115} = 0.716$, $P = 0.476$). A trim-and-fill method also implied that there were no missing effect sizes, consistent with the absence of publication bias.

6.4. Discussion

Overall, our meta-analysis did not detect any strong relationship between urbanization and nest mortality. However, predation rates of artificial nests and of natural nests showed opposite trends in their relationships with urbanization: namely, the chance of natural nests to fail tended to decrease (i.e. the survival of natural nests increased) with increasing urbanization, but the trend in artificial nests was significantly different, and in the opposite direction (i.e. lower survival in more urbanized habitats).

The weak positive trend for a correlation between nest survival and urbanization in natural nests is in line with the 'predator-safe zone hypothesis' (Gering and Blair 1999; Ryder et al. 2010), which assigns the lower predation risk in cities as a principal reason of why certain prey species can thrive in urban habitats. Lower predation rates can be the result of low abundance of nest predators (Møller 2012). However, many potential nest predator species are found in higher abundances in cities than in the surrounding natural habitats (Jokimäki and Huhta 2000;

Haskell et al. 2001). This apparent contradiction is called the ‘nest predation paradox’ (Fischer et al. 2012). This paradox might be resolved in several ways. First, prey species are often extremely abundant in more urban habitats (McKinney 2006). Thus, despite the high absolute numbers of nest predators, their relative abundance to prey can still be low compared to natural habitats (Fischer et al. 2012). Second, urbanization changes predator species composition (Rodewald and Kearns 2011). This shift can mean a decrease in specialized (“strong”) nest predators and an increase in opportunistic (“weak”) nest predators (Stracey 2011). For example, snakes, which are often specialized nest predators, are less abundant in cities than in rural areas (Patten and Bolger 2003). In contrast, house cats, which are both fed by humans and hunt for live prey, and thus are mostly opportunistic nest predators, become more abundant with housing density (Sims et al. 2008), although they might be less common (or less often outdoors) in city centers compared to suburbs. Differences in predator composition can also explain why we found lower predation rates in cities for the cavity nests, but not the open nests: opportunistic nest predators that are common in cities (such as cats, crows or raccoons) are likely to chance upon open nests but unlikely to find cavity nests. Third, potential predators may specialize on different prey in urban than in rural areas as the most abundant prey species might differ between them, which can relax predation pressure on less abundant species (Fischer et al. 2012). Alternatively, in the case of omnivorous predator species, the shift can be towards anthropogenic food sources that are easier to access, which can relax the actual predation pressure on all prey species (Rodewald et al. 2011a). Finally, higher abundance of nest predators in urban habitats can facilitate local adaptation in the behavior of their prey. As high predation pressure in cities should eliminate those individuals that could not effectively defend their nests from predators (either by hiding their nests or actively mobbing predators), the current urban prey population may be better at nest defense and thus can have higher survival rates than rural prey (Stracey 2011).

In contrast to natural nests, we found a decreasing trend in the survival of artificial nests with increasing urbanization. This result is in line with a meta-analysis which revealed more predation on artificial nests with increasing fragmentation of forest habitats (Hartley and Hunter 1998). Also, similarly to our findings, a number of studies showed that predation rates in artificial nests often do not reflect those observed in natural nests (Haskell 1995; Weidinger 2001; Moore and Robinson 2004; Robinson et al. 2005), although one study that used artificial and natural nests in the same conditions did not find significant difference between the two (Blair 2004). The discrepancy between artificial and natural nests may be explained by several different mechanisms. First, our sensitivity analyses on natural nests indicated that predation rates of cavity nests and open nests change differently with urbanization (Table A6.12). Namely, cavity nests are predated significantly less in urban than in rural habitats, while open nests show no such habitat difference. Since the majority of artificial nest studies were conducted on open nests, their results are more comparable to those from natural open nests than to those from hole-like nests (which are also likely to be located high above the ground and exposed to different conditions). Second, as mentioned above, it is hypothesized that local adaptation may make urban bird parents better at nest defense behavior than their non-urban conspecifics (Stracey 2011). As artificial nests are not defended by parents, they may be more likely to be depredated in urban habitats than natural nests. Third, the local adaptation hypothesis also suggests that urban birds are better at hiding their nests from predators (Stracey 2011). As the locations of artificial nests are chosen by the experimenters, rather than the birds themselves, nests may be placed in more conspicuous places in urban habitats, thus predators can find them more easily, resulting in a higher predation rate. Fourth, although artificial nests try to emulate natural nests as much as possible, they might still be perceived by predators as novel compared to natural nests. It has been hypothesized that urban animals show less food neophobia (i.e. are more likely to accept novel food sources) than their rural conspecifics (Sol et al. 2011), and thus non-urban predators may be aversive towards artificial nests. Fifth, some discrepancy between the results of natural versus artificial nest studies may come from the fact that partially predated nests were counted as survived in most natural nest studies, whereas they were counted as predated in artificial nest studies. Partial predation may be more common in cities where the predator is more likely to be interrupted by human disturbance while feeding on a nest. Finally, we cannot exclude the possibility that the real predation pressure on natural nests is higher in cities than in rural habitats, as studies on artificial nests suggest, but the effect is masked by sampling bias. Urban natural nests that were not concealed or defended well enough may already have been predated before the researchers found them, and thus not included in the sample, while this might not be the case in rural habitats. The resulting sampling bias may lead to a seemingly higher predation rate in rural compared to urban habitats.

Our sensitivity analyses on natural nests showed that excluding failures other than predation from the calculation of effect sizes increases the difference in survival rates between urban and non-urban habitats (Table A6.12). This indicates that nest failures other than predation might be more common in urban than in rural habitats, leveling out the lower nest predation rate and resulting in a more similar overall nest failure rates in urban and rural habitats. For example, mortality due to vandalism from humans is more likely to happen in urban habitats where humans are more abundant. Higher human disturbance may also increase the chance of nest abandonment compared to habitats with lower human disturbance (Carney and Sydeman 1999). Urban areas are also characterized by higher chemical pollution (e.g., Mayer, 1999; Wei and Yang, 2010), which can accumulate in birds (Hofer et al. 2010), and ultimately result in increased mortality of chicks (Fry 1995). Finally, starvation due to lower quantity or quality of food can also lead to increased chick mortality in cities (Seress and Liker 2015). These possibilities may be interesting to explore in a future meta-analysis.

In conclusion, our results show that natural nests tend to be less predated in urban habitats than in rural habitats, but this trend is not reflected by studies on artificial nests. We have several recommendations for future studies addressing the relationship of urbanization and nest predation. First, we suggest that the cause of nest failure should be identified as precisely as possible, because both predation and other forms of mortality (weather, nest abandonment, vandalism by humans) can vary with urbanization, affecting the overall nest survival. Second, to identify whether variation is due to differences between species, multiple populations of the same species should be studied, and studies should preferably include data from multiple species. Finally, as patterns derived from studies using artificial nests often do not qualitatively reflect those derived from natural nests, researchers should perform studies where artificial and natural nests with similar characteristics are monitored within the same area (e.g., Blair, 2004), and investigate sampling bias. Such validation is important to draw firm conclusions regarding the level of predation in urban versus rural areas in future studies.

CHAPTER 7:
SUMMARY AND GENERAL CONCLUSIONS

In my thesis, I explored several differences between urban and non-urban individuals of two bird species, the house sparrow and the great tit, in their fear responses towards hostile and non-hostile humans and towards non-human predators, and compared predation pressure on avian nests between urban and non-urban habitats. In this final chapter, I summarize the results and compare them among studies, and draw some general conclusions.

I found evidence that urban individuals of both species are less fearful towards humans than their rural conspecifics, as shown by the lower flight initiation distances of urban house sparrows (***Chapter 3***) and the shorter return latencies and higher number of nest visits of urban compared to rural great tits in presence of humans (***Chapter 5***). These two results fit very well in the general pattern that urban animals are bolder towards humans than rural animals (Samia et al. 2015; Myers and Hyman 2016; Carrete and Tella 2017), confirming that tolerance of human disturbance is ubiquitous in urban habitats. Furthermore, as my two studies investigated fear from humans with different methods in different situations (flight initiation distance in wintering flocks versus nest provisioning behavior in breeding pairs), it appears that the higher risk taking of urban birds towards humans is present in several contexts.

Despite the overwhelming evidence that urban and non-urban animals differ in their behavioral responses to humans, little is known whether it is due to behavioral plasticity or due to intrinsic differences via differential colonization or micro-evolutionary selection (Miranda 2017). In ***Chapter 3***, I found no significant difference in the initial response to a novel human disturbance between house sparrows captured from urban and non-urban habitats: sparrows from both habitat types were equally likely to hide when they were disturbed for the first time. This suggests that in a novel situation, they are equally fearful from humans. However, I also found that both urban and rural sparrows reduced their fear from humans over time, but this habituation was faster in urban than rural sparrows, as it took fewer trials for the former to minimize their hiding time. These results suggest that reduced fear from humans in urban house sparrows is primarily due to behavioral plasticity, rather than differences in intrinsic boldness as predicted by differential colonization and/or local adaptation. A recent study also showed that captive house sparrows generally show fast habituation to both humans and novel objects, supporting the idea that this species has particularly flexible behavior (Moldoff and Westneat

2017). However, studies on other avian species found consistent behavior towards humans and habitat choice based on behavioral type, rather than plastic response to the level of human disturbance (Holtmann et al. 2017; Sprau and Dingemanse 2017). This suggests that intrinsic differences between individuals may also play an important role in urbanization, and/or that the relative importance of the two mechanisms is species- or context-dependent.

In our study, rural house sparrows were less fearful from the familiar non-hostile person than from the familiar hostile or unfamiliar persons (***Chapter 4***), but urban house sparrows showed no such distinction, despite its potential benefits. This result is, at first, surprising, as urban animals are both often considered cognitively superior to non-urban animals, and they have more experience with humans. However, there are several possible explanations why rural birds could be better at recognizing humans and/or more motivated to adjust their behavior based on past experiences with different people: in farmlands, although the overall number of encounters with humans is lower, the probability of encountering the same humans may be higher; people living in farms might be less neutral in their behavior towards birds (especially house sparrows, which are often considered as pests); and memorizing fewer people is cognitively less challenging.

In contrast to sparrows, I found no signs of human recognition in great tits: neither urban birds nor forest birds showed differential responses to potentially dangerous and non-dangerous humans (***Chapter 5***). The apparent contrast between the results of the two studies could be due to differences between the two species, originating from their evolutionary past. House sparrows have been living in commensalism with humans for thousands of years (Sætre et al. 2012), whereas great tits colonized anthropogenic habitats fairly recently (Møller et al. 2012), therefore the former had more time to evolve the ability to recognize individual humans. Additionally, house sparrows are often seen as pests by the public, especially in farmlands, thus differentiating between hostile and non-hostile humans could be more crucial for them than for great tits, which are usually seen as pleasant birds and thus less likely to experience hostility by humans.

However, it is also possible that rather than an actual between-species difference, the contrast between house sparrows and great tits in human recognition is due to differences in the study designs. First, our non-urban house sparrows were from villages and farmlands, whereas our non-urban great tits were from forests. It is possible that the relationship between urbanization and the ability to recognize humans is non-linear, with the best human recognition abilities at medium urbanization levels. Specifically, birds from cities with high human population density may not differentiate between people (because of the high cognitive cost of memorizing too many humans, the relatively few repeated encounters with the same person, and/or the neutral attitude of humans towards birds), nor do birds from forests with no resident human population (because of the very few overall encounters with humans). However, birds from farms with low, but non-negligible resident human population density may be good at recognizing humans due to the high chance of repeated encounters with the same persons, and the more variable, and often hostile attitude towards birds. Second, in the study with great tits, the two people were a hostile and an unfamiliar person. Our house sparrows did not differentiate between the familiar hostile and the unfamiliar person either; instead, they showed reduced fear responses to the familiar non-hostile person. Thus, it is possible that both great tits and house sparrows consider unfamiliar people as potentially hostile, and show no further sensitization following repeated hostile disturbances. This possibility is contrasted by studies on other avian species that found that they sensitize to and specifically recognize people who disturbed their nests earlier (Levey et al. 2009; Lee et al. 2011) or captured them before (Marzluff et al. 2010). Third, differentiation between humans can be context-dependent: it is possible that during breeding season, the drive to feed the offspring is high even when there is a potentially dangerous human present, whereas during the winter, in captivity, the birds can afford avoiding potentially dangerous or unfamiliar humans. Finally, there might be differences in the cues the animals used to recognize the different people: while sparrows may have focused on the facial features of the different humans (i.e. masks), great tits could have used other cues, such as the presence of the stick we used during nest checks for reaching and detaching the nest boxes as a cue to expect a disturbing human action. As neither the familiar nor the unfamiliar person carried the stick during the human disturbance tests, the birds may have perceived neither of them more dangerous than the other.

I did not investigate the ability of birds to recognize and respond to benevolent humans. However, there is anecdotal evidence that at least some birds recognize people who feed them (Howard 1953), and experimental studies on domestic animals such as rabbits show that they recognize people associated with positive stimuli such as food (Davis and Gibson 2000). Therefore investigating this ability in birds along the urban-rural gradient is an interesting direction for future research.

I also found that urban great tits, compared to forest-dwelling conspecifics, take more risk when they are presented a sparrowhawk mount (***Chapter 5***), implying that they are less afraid of the sparrowhawk and/or more motivated to feed their offspring despite its presence. Although I did not test the same question on house sparrows, earlier studies on captive house sparrows indicated that urban house sparrows were more fearful from sparrowhawks than rural house sparrows (Bókony et al. 2012a), although this contrast was only present in older sparrows, whereas younger, inexperienced sparrows showed the opposite effect (Seress et al. 2011). Thus, the urban-rural contrast in response to the sparrowhawk seems to be in the opposite direction for great tits and for (at least old) house sparrows. Both species are hunted by sparrowhawks; however, it is possible that in cities, sparrowhawks prefer to hunt the larger, less agile sparrows, whereas in forest habitats, where sparrows are not present, sparrowhawks pose a greater threat on great tits. Notably, a study on urban sparrowhawks in Scotland showed that 26.7% of their prey were house sparrows and only 4.3% were great tits (McGrady 1991), whereas another study on rural (forest and farmland) sparrowhawks in Poland found that 9.4% of their prey consisted of great tit, but they did not find a single sparrow among their prey (Zawadzka and Zawadzki 2001). Another factor that might cause the difference is a seasonal effect: the earlier house sparrow studies were conducted in winter, whereas our great tit study was performed in the breeding season. Sparrowhawks can reach higher densities in cities in winter compared to spring and summer (Seress et al. 2011), perhaps because they use forest habitats for breeding, but move to cities outside the breeding season due to less harsh winters. This means that sparrowhawks may pose a greater threat to forest birds in the spring and to urban birds in the autumn and winter.

Despite the fact that urban great tits were more risk-taking towards both sparrowhawks and humans than forest tits were, we found no correlation between the two behaviors, neither within nor across habitat types. This indicates that this contrast between urban and rural birds is not likely to be due to a general risk-taking response (i.e. a behavioral syndrome), but rather due to specific responses to each type of threat. Based on this, I can generalize that even if two groups of animals show similar contrasts on average for two different forms of behavior, this does not necessarily mean that the two behaviors are driven by the same proximate mechanism.

In the meta-analysis, I found that mortality of bird nests due to predation is higher in rural than in urban habitats, but this is not reflected by experimental studies on artificial nests, where urban nests were depredated more often than rural nests (***Chapter 6***). This discrepancy may be due to several differences between the setups of the two study types, including inherent differences such as the lack of nest defense in artificial nests, as well as biased choices by the experimenters regarding nest placement and the interpretation of partially predated nests. The lower mortality of natural nests in cities, combined with the weaker responses to sparrowhawk by great tits, may point towards lower overall predation risk in cities both on adult birds and their nests; however, we need to be careful with this generalization, as the results with artificial nests suggest the contrary.

The discrepancy between artificial and natural nest studies, the lack of correlation between responses to humans and responses to sparrowhawk in great tits, and the differences between great tits and house sparrows in human recognition and responses to sparrowhawk, imply that conclusions about urbanization's overall effect on predation pressure and anti-predator behavior should be drawn carefully. Results can depend on both the study system and the study design. Urbanization poses different challenges to each species; even common, intuitive assumptions, like urban habitats being more complex than natural habitats, largely depend on the ecological characteristics of the study species (Griffin et al. 2017). Furthermore, different species may use different behavioral and life-history strategies to cope with the ecological challenges of urbanization. Differences between species may make some species better urban exploiters than others (Evans et al. 2011), but urban populations may adapt to urban habitats in various ways (Macías Garcia et al. 2017), and the relative role of between-individual and within-individual behavioral variation, i.e. intrinsic differences and behavioral plasticity, can also vary among species (Miranda 2017). This, in turn, affects interspecific interactions, including predation and competition. Furthermore, even studies on the same species may come to contrasting conclusions due to differences in the study design.

Because of the above reasons, drawing broad, general conclusions from specific results can be very misleading. A meta-analytical approach, like the one I used in ***Chapter 6***, is a good way to explore both general trends and discrepancies, which can be used for generating further hypotheses to test. It seems that there are general trends that are present across a broad range of species, such as reduced fearfulness from humans in cities, but many other patterns, like recognition of individual humans, responses to different types of threats, and nest mortality due to predation, can show broad variation across study systems. As urbanization is currently a hot topic in ecology, we may expect new, exciting results in the near future.

Ethical note: All procedures of the studies included in this thesis were in accordance with Hungarian laws and licensed by the Middle Transdanubian Inspectorate for Environmental Protection, Natural Protection and Water Management (permission number: 31559/2011).

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THESIS POINTS

1. House sparrows in urban habitats had shorter flight initiation distances from humans than birds in rural habitats (i.e. farmlands), and great tits breeding in urban habitats reduced their nest visit rates to a lesser extent than great tits in forests when a human was present under their nest box. Both indicate that urban birds are less fearful of humans.
2. When taken to captivity, urban and non-urban sparrows showed similar initial response to human disturbance, but urban sparrows habituated faster to repeated disturbance. This implies that the difference between urban and rural sparrows in their fear from humans is more likely due to habituation than due to selection for intrinsic differences.
3. Following repeated encounters with two differently threatening persons in captivity, rural sparrows became less fearful from the non-hostile than the hostile or an unfamiliar person, but urban sparrows made no such distinction. This suggests that rural sparrows are better at recognizing individual humans and/or such an ability is more advantageous in rural habitats such as farms and villages.
4. Neither urban nor forest great tits differentiated between an unfamiliar and a familiar, previously hostile person, indicating that recognizing humans and/or adjusting behavior to previous experiences with different persons, may have no ecological relevance for great tits in these habitat types.
5. Urban great tits responded less fearfully to sparrowhawk than non-urban great tits during brood care, which may be explained by lower predation risk in cities, or by environmental constraints.
6. There was no correlation in great tits between the response to human disturbance and the response to sparrowhawk, suggesting that the differences between urban and rural birds in these two responses are likely to be specific to the type of threat rather than being part of a general fearfulness syndrome.
7. In a meta-analysis, I showed that natural bird nests are less predated in more urbanized than in less urbanized habitats, but artificial bird nests are more frequently predated in cities. This discrepancy can be due to differences in experimental design (e.g., cavity nests have been more commonly studied in natural nest studies), intrinsic differences between the two nest types (e.g., lack of parental nest defense in artificial nests), or sampling bias (e.g., natural nests that were predated at an early stage not being found).

TÉZISPONTOK

1. Városi élőhelyeken a házi verebek embertől való menekülési távolsága rövidebb volt, mint vidéki élőhelyeken (falvak szélén, tanyákon), és a városban fészkelő széncinegék kisebb mértékben csökkentették le az odúlátogatásaik számát, amikor egy ember áll az odú alatt, mint erdőben fészkelő fajtársaik. Mindkettő arra utal, hogy a városi madarak kevésbé félnek az embertől.
2. Fogságban a városi és vidéki verebek első alkalommal egyformán reagáltak az emberi zavarásra, de az ismételt zavaráshoz a városiak gyorsabban habituálódtak. Ez arra utalhat, hogy a városi és vidéki madarak közti különbség az embertől való félősségben inkább habituáció, mint a madarak közti egyedi eltérésekre ható szelekció következménye.
3. Egy ellenséges és egy nem ellenséges emberrel való ismételt találkozásokat követően a vidéki verebek kevésbé féltek az utóbbitól, mint az előbbitől vagy egy ismeretlen személytől, míg a városiak nem tettek ilyen különbséget. Ebből arra következtethetünk, hogy a vidéki madarak nagyobb mértékben képesek különbséget tenni az emberek között, és/vagy ez a képesség vidéki élőhelyeken előnyösebb.
4. Sem a városi, sem a vidéki széncinegék nem tettek különbséget egy ismeretlen és egy ismerős, ellenséges ember közt, ami arra utalhat, hogy az emberfelismerés és/vagy az emberrel szembeni viselkedés korábbi tapasztalatokhoz igazítása nem jelent a széncinegék számára ökológiai előnyt ezen a két élőhelyen.
5. A városi széncinegék gyengébb félelmi választ mutattak karvalyra, mint erdei fajtársaik, aminek oka lehet kisebb predációs kockázat városban, de más környezeti kényszer is.
6. A széncinegék karvalyra és az emberre adott viselkedési válaszai nem korreláltak egymással, ami arra utal, hogy a város-vidék különbség ebben a két viselkedésben inkább veszélyforrás-specifikus, mintsem egy általános félősségi szindróma része.
7. Egy metaanalízis során azt találtam, hogy a természetes madárfészkek ritkábban esnek predáció áldozatául urbanizáltabb, mint nem urbanizált élőhelyeken, míg a mesterséges fészkek predációja városban gyakoribb. Ennek oka lehet módszertani eltérés (pl. a vizsgált természetes fészkek közt gyakoribbak az odúfészkek), a fészektípus sajátosságaiból adó eltérés (pl. a fészekvédő viselkedés hiánya mesterséges fészkeknél), vagy mintavételi torzítás (pl. a korai szakaszban zsákmányul esett fészkek kimaradnak a vizsgálatból).

PUBLICATONS

1. Papers included in present thesis

1) Ernő Vincze, Sándor Papp, Bálint Preiszner, Gábor Seress, András Liker & Veronika Bókony (2015): Does urbanization facilitate individual recognition of humans by house sparrows? Animal Cognition 18: 291-298
2) Ernő Vincze, Sándor Papp, Bálint Preiszner, Gábor Seress, Veronika Bókony & András Liker (2016): Habituation to human disturbance is faster in urban than rural house sparrows. Behavioral Ecology 27: 1304-1313
3) Ernő Vincze, Gábor Seress, Malgorzata Lagisz, Shinichi Nakagawa, Niels J. Dingemanse & Philipp Sprau (2017): Does urbanization affect predation of bird nests? A meta-analysis. Frontiers in Ecology and Evolution 5:29
4) Ernő Vincze, Veronika Bókony, Ivett Pipoly, Gábor Seress, Bálint Preiszner, Sándor Papp, Brigitta Németh & András Liker (in prep.): Responses to sparrowhawks and familiar and unfamiliar humans by urban and non-urban great tits: is anti-predator risk taking general or threat-specific?

2. Papers not included in present thesis

1) Veronika Bókony, Veronika, Ádám Z. Lendvai, Csongor I. Vágási, Laura Pătraş, Péter L. Pap, József Németh, Ernő Vincze, Sándor Papp, Bálint Preiszner, Gábor Seress & András Liker, (2014): Necessity or capacity? Physiological state predicts problem-solving performance in house sparrows. Behavioral Ecology 25: 124–35
2) Ákos Pogány, János Heszberger, Zita Szurovecz, Ernő Vincze, Tamás Székely (2014a): An infrared motion detector system for lossless real-time monitoring of animal preference tests. Acta Biologica Hungarica 65 (4): 385–95
3) Ákos Pogány, Zita Szurovecz, Ernő Vincze, Zoltán Barta, Tamás Székely (2014b): Mate preference does not influence reproductive motivation and parental cooperation in female zebra finches. Behaviour 151 (12-13): 1885–1901
4) Ivett Pipoly, Bálint Preiszner, Gábor Seress, Ernő Vincze, András Liker. (2014): Éghajlatváltozás erdőn, mezőn: a vadon élő állatok kutatásának tanulságai. Iskolakultúra 11-12: 103-114
5) Jodie M.S. Crane, Joel L. Pick, Alice J. Tribe, Ernő Vincze, Ben J. Hatchwell, Andrew F. Russell (2015): Chestnut-crowned babblers show affinity for calls of removed group members: a dual playback without expectancy violation Anim Behav 104:51–57
6) Sándor Papp, Ernő Vincze, Bálint Preiszner, András Liker, Veronika Bókony (2015): A comparison of problem-solving success between urban and rural house sparrows. Behavioral Ecology and Sociobiology 69: 471–80.
7) Bálint Preiszner, Sándor Papp, Ernő Vincze, Veronika Bókony, András Liker (2015): Does innovation success influence social interactions? An experimental test in house sparrows. Ethology 121: 661–73
8) Bálint Preiszner, Sándor Papp, Ivett Pipoly, Gábor Seress, Ernő Vincze, András Liker, Veronika Bókony (2017): Problem-solving performance and reproductive success of great tits in urban and forest habitats. Animal Cognition 20: 53–63

9) Veronika Bókony, Ivett Pipoly, Krisztián Szabó, Bálint Preiszner, Ernő Vincze, Sándor Papp, Gábor Seress, Tamás Hammer, András Liker (2017): Innovative females are more promiscuous in great tits (Parus major). Behavioral Ecology 28:579-588

10) Gábor Seress, Ernő Vincze, Ivett Pipoly, Tamás Hammer, Sándor Papp, Bálint Preiszner, Veronika Bókony, András Liker (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.

11) Gábor Seress, Tamás Hammer, Veronika Bókony, Ernő Vincze, Bálint Preiszner, Ivett Pipoly, Csenge Sinkovics, Karl L. Evans, András Liker (2018): Impact of urbanization on abundance and phenology of caterpillars and consequences for breeding in an insectivorous bird. Ecological Applications (in press).

3. Conference talks and posters

1) Vincze, E., Pogány, Á., Szurovecz, Z., Kosztolányi, A., Barta, Z., Székely, T., 2011. Sexual selection of a personality trait: Assortative mate choice for boldness in zebra finches (in Hungarian), 13th Congress of the Hungarian Ethological Society, Debrecen, Hungary; conference talk

2) Vincze, E., Pogány, Á., Szurovecz, Z., Kosztolányi, A., Barta, Z., Székely, T., 2011. Sexual selection of a personality trait: Assortative mate choice for boldness in zebra finches; ASAB Winter Meeting 2011, Zoological Society of London, London, United Kingdom; poster

3) Pogány, Á., Vincze, E., Szurovecz, Z., Kosztolányi, A., Riebel, K., Barta, Z., Székely, T. 2012. Assortative mate choice for boldness in zebra finches. 14th International Behavioral Ecology Congress, Lund, Sweden; conference talk

4) Vincze, E., Bókony, V. & Liker, A. 2012. Behavioural responses to humans in house sparrows: repeatability, individual recognition and urbanization 14th Congress of the Hungarian Ethological Society, Kolozsvár, Romania; conference talk

5) Vincze, E., Bókony, V. & Liker, A. 2012. Learning in a probem-solving task is related to urbanization and other individual traits in house sparrows. (in Hungarian) 9th Congress of Hungarian Ecologists, Keszthely, Hungary; conference talk

6) Vincze, E., Bókony, V. & Liker, A. 2012. Learning in a probem-solving task is related to urbanization and other individual traits in house sparrows. (in Hungarian) 1st Conference of Doctoral Schools of Environmental Sciences, Budapest, Hungary; conference talk

7) Vincze, E., Bókony, V. & Liker, A. 2012 Learning in a problem-solving task is related to body condition and risk taking in house sparrows. ASAB Interdisciplinary Workshop 2012: Physical Cognition & Problem Solving, Birmingham, United Kingdom; conference talk

8) 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; conference talk

9) 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; conference talk

10) 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; poster
11) Vincze, E., Bókony, V. & Liker, A. 2013. Behavioural responses to humans in house sparrows: repeatability, individual recognition and urbanization. (in Hungarian) 3. Congress of Ornithology in Győr-Moson-Sopron, Kapuvár, Hungary; conference talk
12) Vincze, E., Bókony, V. & Liker, A. 2013. Behavioural responses to humans in house sparrows: repeatability, individual recognition and urbanization. Science for Sustainability, Győr, Hungary; conference talk
13) 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; poster
14) 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; poster
15) 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; plenary talk
16) 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; conference talk
17) Papp, S., Hammer, T., Vincze, E., Preiszner, B., Pipoly, I., Seress, G., Liker, A. & Bókony, V. 2014. Effects of urbanization on neophobia and problem-solving success in house and tree sparrows. (in Hungarian) 16th Congress of the Hungarian Ethological Society, Tihany, Hungary; conference talk
18) 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; conference talk
19) 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; conference talk
20) 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. VII. European Conference on Behavioural Biology, Prague, Czech Republic; conference talk
21) 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; poster

22) 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; poster
23) 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; conference talk
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APPENDICES

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APPENDICES TO CHAPTER 3

Table A3.1: *Habitat characteristics and sample sizes of the 15 sites. Habitat characteristics were scored with the UrbanizationScore image-analysis software* (Seress et al. 2014)*, see Methods for further details. Abbreviations: CO: cohort ID; MB: mean building density; B50: number of cells with >50% buildings; R: number of cells with roads; MV: mean vegetation density, V50: number of cells with >50% vegetation; HPD: human population density (number of residents / km^2); PC: principal component score calculated from the above 6 variables ("urbanization score"); UC: urbanization category; FN: number of flocks with FID recorded at the site; FS: mean number of individual sparrows in a flock within a site; CI: number of individuals captured at a site.*

CO	Site	Latitude	Longitude	MB	B50	R	MV	V50	HPD	PC	UC	FN	FS	CI
1.	Ajka	47° 5'49.60"N	17°32'18.89"E	1.04	31	55	1.39	49	334.6	0.296	urban	8	8	7
1.	Veszprém	47° 5'6.91"N	17°54'11.09"E	1.64	67	94	1.15	15	495.2	2.46	urban	9	6.89	5
2, 8.	Szentgál	47° 6'9.65"N	17°42'14.54"E	0.06	0	15	2	100	6	-3.269	rural	10	20.6	10
2.	Öskü	47° 9'48.18"N	18° 4'19.85"E	1.08	37	56	1.54	54	47.7	-0.121	rural	9	6.67	4
3.	Dunaújváros	46°57'51.24"N	18°55'49.44"E	1.6	71	91	1.12	15	1050.3	2.608	urban	9	40	7
3.	Székesfehérvár	47°11'22.63"N	18°24'28.92"E	1.79	79	100	1.05	10	723.1	3.043	urban	12	7.87	5
4.	Bánd	47° 7'18.39"N	17°47'34.95"E	0.22	4	26	1.94	94	64.9	-2.432	rural	9	11.88	5
4.	Salföld	46°50'13.11"N	17°32'57.19"E	0.23	5	23	1.83	83	12.4	-2.47	rural	14	23	5
5.	Balatonfüred	46°57'17.98"N	17°53'0.32"E	1.54	65	91	1.27	27	278.9	1.956	urban	16	9.47	5
5.	Siófok	46°54'31.11"N	18° 3'24.31"E	1.45	53	92	1.11	11	182	2.032	urban	10	15	6
6.	Babat	47°37'23.17"N	19°22'47.76"E	0.16	0	17	1.92	92	4	-3.059	rural	11	11.18	4
6.	Üllő	47°20'41.41"N	19°19'6.81"E	0.22	4	22	1.92	92	3.58	-2.913	rural	10	10.05	10
7.	Budapest, District IX-X.	47°28'15.10"N	19° 6'39.03"E	0.97	25	77	1.39	42	3757.65	0.93	urban	15	6.07	6
7.	Budapest, District XI	47°27'53.12"N	19° 1'19.43"E	1.47	61	86	0.85	8	4315.5	2.921	urban	12	6.52	8
8.	Seregélyes-szőlőhegy	47° 6'33.01"N	18°36'58.55"E	0.46	11	31	1.88	88	58.7	-1.983	rural	9	12.33	10

Table A3.2: *Initial full models corresponding to Tables 3.1 and 3.2. For the interpretation of the parameter estimates (b), see the notes at Table 3.1.*

A) **Flight initiation distance (corresponding to Table 3.1)**

Fixed effects	***b***	± ***SE***	***df***	***t***	***P***
Intercept (last, urban, ground, no other species)	0.433	± 1.354	154	0.320	0.749
Flight order (first vs. last)	0.680	± 0.138	154	4.923	<0.001
Habitat (rural vs. urban)	3.750	± 0.956	13	3.922	0.002
Flock size	0.100	± 0.032	142	3.160	0.002
Position (perched vs. ground)	-2.750	± 0.774	142	-3.555	0.001
Date	-0.033	± 0.013	142	-2.479	0.014
Starting distance	0.427	± 0.045	142	9.494	<0.001
Time of day	0.002	± 0.002	142	1.331	0.185
Other species (yes vs. no)	0.398	± 0.928	142	0.428	0.669
Habitat × Flight order	0.690	± 0.368	154	1.876	0.063
Random effects	***SD***				
Site	1.539				
Group ID in Site	2.413				
Residual variance	0.902				

B) **Hiding frequency in the first trial (corresponding to Table 3.2A)**

	b	± ***SE***	***df***	***t***	***P***
Intercept (urban, position: shelf 1, column 1, male, not fasted)	-4.828	± 2.076	80	-2.325	0.023
Habitat (rural vs. urban)	0.983	± 0.785	6	1.252	0.257
Position (shelf 2 vs. 1)	-0.067	± 0.342	80	-0.196	0.845
Position (shelf 3 vs. 1)	0.707	± 0.362	80	1.952	0.054
Position (column 2 vs. 1)	0.021	± 0.464	80	0.046	0.964
Position (column 3 vs. 1)	0.644	± 0.496	80	1.299	0.198
Position (column 4 vs. 1)	0.525	± 0.441	80	1.191	0.237
Position (column 5 vs. 1)	0.829	± 0.427	80	1.939	0.056
Sex (female vs. male)	0.354	± 0.336	80	1.054	0.295
Treatment group (fasted vs. not fasted)	-0.340	± 0.351	80	-0.968	0.336
Body condition	0.074	± 0.072	80	1.027	0.308
Random effects	***SD***				
Cohort ID	0.957				
Residual variance	0.341				

C) **Hiding frequency in all 8 trials (corresponding to Table 3.2B)**

	b	**± *SE***	***df***	***t***	***P***
Intercept (urban, trial 1, position: shelf 1, column 1, male, not fasted, can access food)	-1.863	± 2.295	676	-0.812	0.417
Trial number	-0.337	± 0.042	676	-8.097	<0.001
Habitat (rural vs. urban)	0.530	± 0.614	6	0.863	0.421
Position (shelf 2 vs. 1)	-0.163	± 0.372	80	-0.440	0.662
Position (shelf 3 vs. 1)	0.915	± 0.403	80	2.270	0.026
Position (column 2 vs. 1)	-0.378	± 0.515	80	-0.735	0.465
Position (column 3 vs. 1)	-0.197	± 0.564	80	-0.348	0.728
Position (column 4 vs. 1)	-0.379	± 0.507	80	-0.748	0.457
Position (column 5 vs. 1)	0.154	± 0.480	80	0.320	0.750
Sex (female vs. male)	0.182	± 0.344	80	0.529	0.598
Treatment group (fasted vs. not fasted)	-0.358	± 0.428	80	-0.836	0.406
Body condition	-0.012	± 0.083	80	-0.148	0.883
Access to food (no vs. yes)	-0.078	± 0.189	676	-0.414	0.679
Trial number × Habitat	0.170	± 0.048	676	3.518	0.001
Random effects	***SD***				
Cohort ID	0.708				
Bird ID in Cohort ID	1.279				
Residual variance	0.327				

D) **Reactivity in all 8 trials (corresponding to Table 3.2C)**

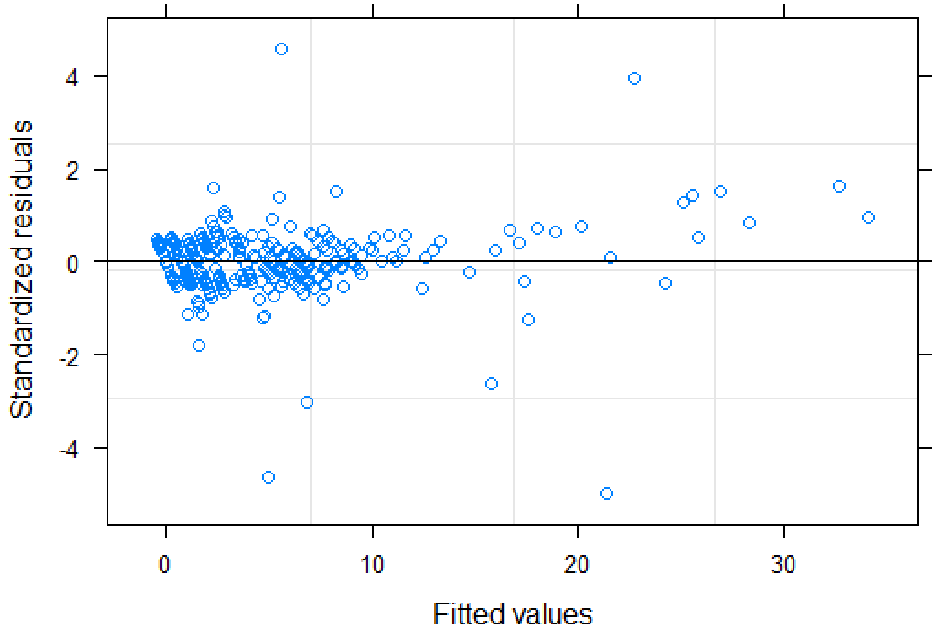
	b	**± *SE***	***df***	***t***	***P***
Intercept (urban, trial 1, position: shelf 1, column 1, male, not fasted, can access food)	-0.464	± 3.387	676	-0.137	0.891
Trial number	-1.316	± 0.080	676	-16.417	<0.001
Habitat (rural vs. urban)	0.743	± 1.030	6	0.721	0.498
Position (shelf 2 vs. 1)	-0.184	± 0.541	80	-0.340	0.735
Position (shelf 3 vs. 1)	0.461	± 0.608	80	0.759	0.450
Position (column 2 vs. 1)	0.234	± 0.779	80	0.301	0.764
Position (column 3 vs. 1)	0.505	± 0.838	80	0.602	0.549
Position (column 4 vs. 1)	-0.458	± 0.772	80	-0.593	0.555
Position (column 5 vs. 1)	0.581	± 0.733	80	0.792	0.431
Sex (female vs. male)	0.095	± 0.502	80	0.190	0.850
Treatment group (fasted vs. not fasted)	-1.212	± 0.675	80	-1.795	0.076
Body condition	0.096	± 0.123	80	0.780	0.438
Access to food (no vs. yes)	0.985	± 0.421	676	2.340	0.020
Trial number × Habitat	0.249	± 0.107	676	2.321	0.021
Random effects	***SD***				
Cohort ID	1.115				
Bird ID in Cohort ID	1.851				
Residual variance	3.418				

E) **Recovery in all 8 trials (corresponding to Table 3.2D)**

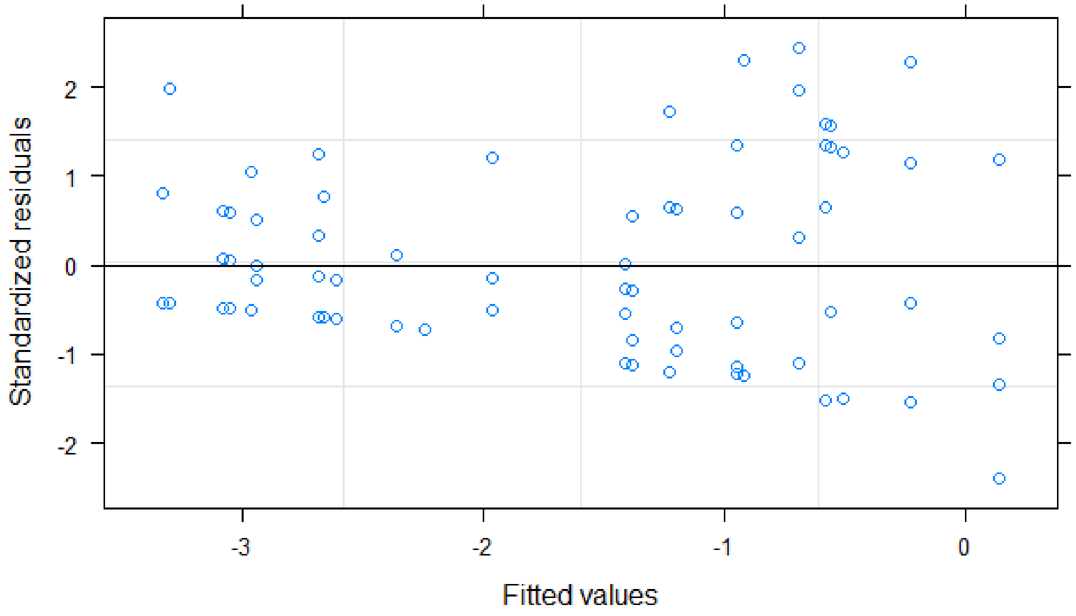
	b	**± *SE***	***df***	***t***	***P***
Intercept (urban, trial 1, position: shelf 1, column 1, male, not fasted, can access food)	-0.503	± 0.206	676	-2.435	0.015
Trial number	-0.006	± 0.004	676	-1.674	0.095
Habitat (rural vs. urban)	0.089	± 0.059	6	1.505	0.183
Position (shelf 2 vs. 1)	-0.004	± 0.033	80	-0.109	0.913
Position (shelf 3 vs. 1)	0.096	± 0.037	80	2.588	0.012
Position (column 2 vs. 1)	-0.062	± 0.048	80	-1.303	0.196
Position (column 3 vs. 1)	-0.025	± 0.051	80	-0.483	0.630
Position (column 4 vs. 1)	-0.072	± 0.047	80	-1.516	0.134
Position (column 5 vs. 1)	0.009	± 0.045	80	0.203	0.840
Sex (female vs. male)	-0.007	± 0.031	80	-0.230	0.819
Treatment group (fasted vs. not fasted)	0.001	± 0.040	80	0.023	0.982
Body condition	0.004	± 0.008	80	0.493	0.623
Access to food (no vs. yes)	-0.023	± 0.019	676	-1.200	0.231
Trial number × Habitat (rural vs. urban)	0.000	± 0.005	676	0.047	0.963
Random effects	***SD***				
Cohort ID	0.068				
Bird ID in Cohort ID	0.124				
Residual variance	0.150				

Figure A3.1 *Model diagnostic plots (standardized residuals versus fitted values) for the final models, corresponding to Tables 3.1 and 3.2.*

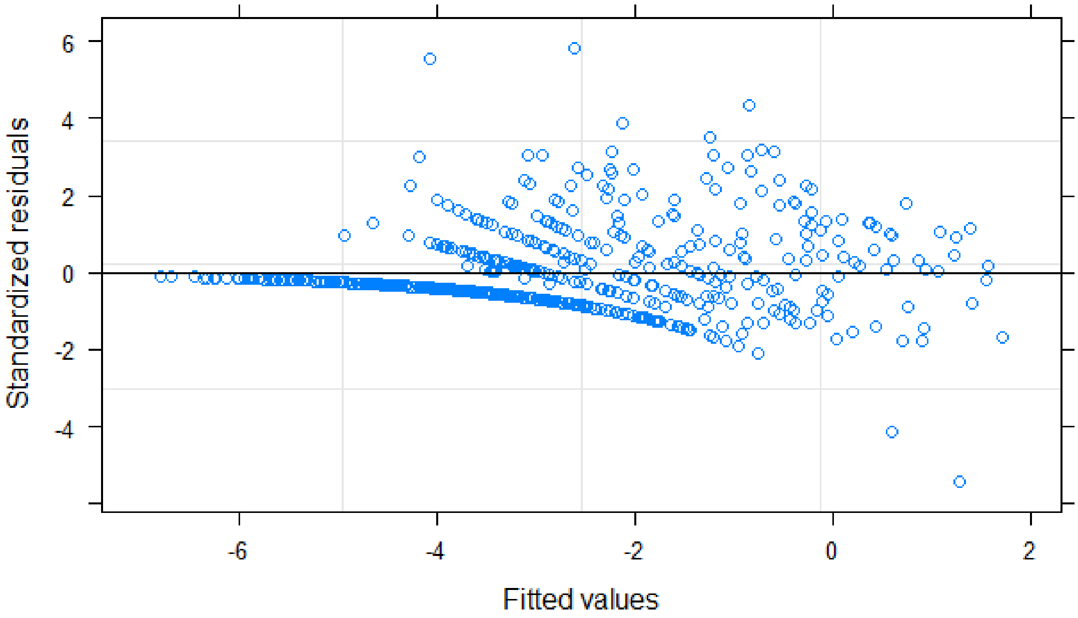
A) Flight initiation distance (corresponding to Table 3.1)



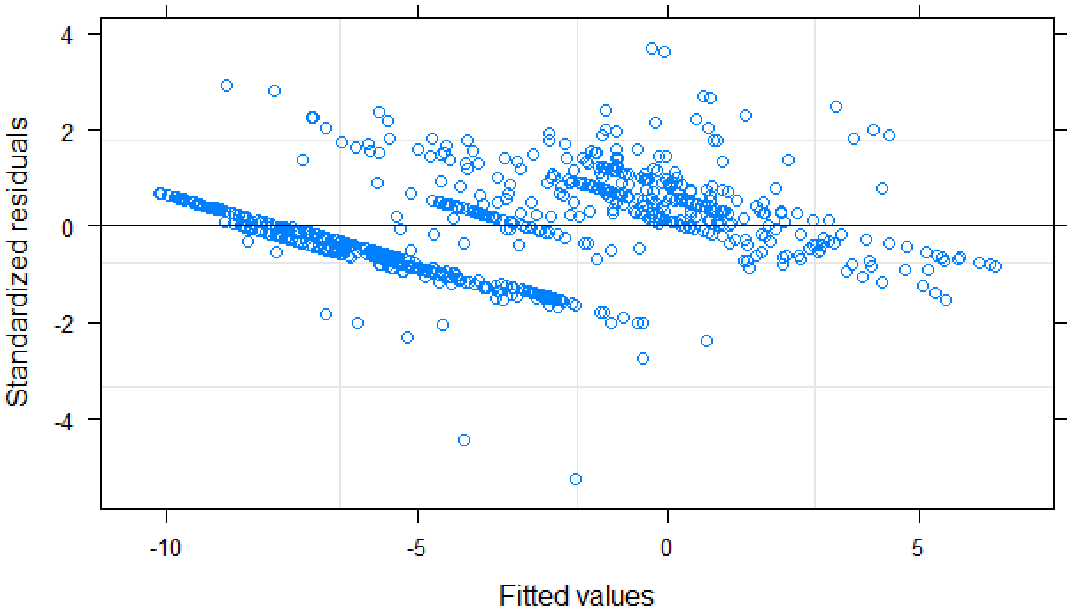
B) Hiding frequency in the first trial (corresponding to Table 3.2A)



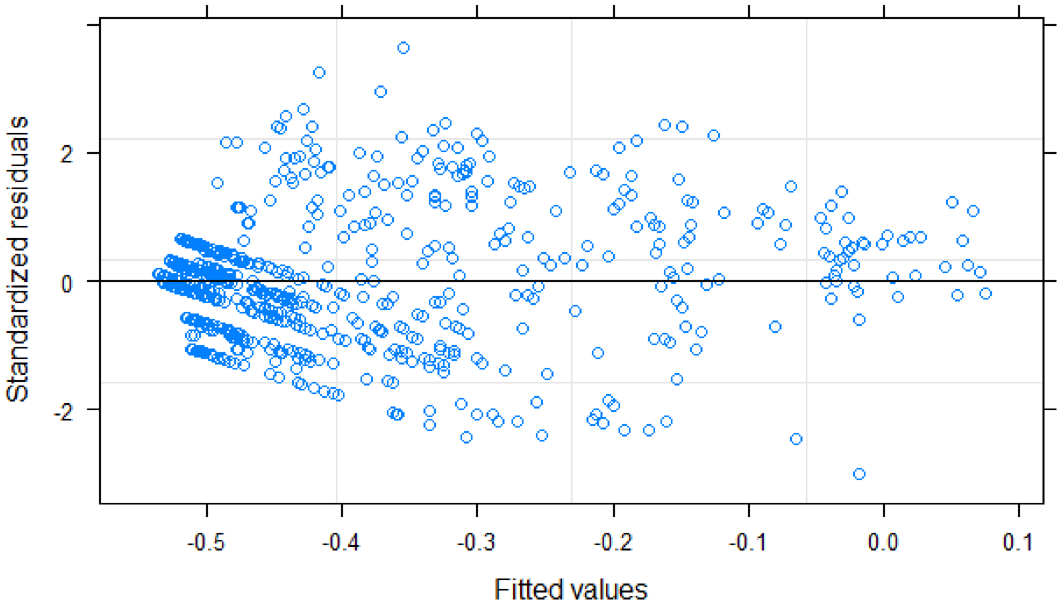
C) **Hiding frequency in all 8 trials (corresponding to Table 3.2B)**



D) **Reactivity in all 8 trials (corresponding to Table 3.2C)**



E) Recovery in all 8 trials (corresponding to Table 3.2D)



Appendices to Chapter 4

Table A4.1: *Order of training sessions (days 1-4 each week) and test sessions (day 5), and mask-treatment combinations for each cohort*

Cohort 1: Veszprém (urban) + Ajka (urban)

Masks: non-hostile - C; hostile - B; unfamiliar - A

time\date	2012-01-09	2012-01-10	2012-01-11	2012-01-12	2012-01-13
8:30	hostile	hostile	non-hostile	non-hostile	hostile
10:30	hostile	non-hostile	hostile	hostile	unfamiliar
12:30	non-hostile	non-hostile	non-hostile		non-hostile
14:30	non-hostile	hostile	hostile		

Cohort 2: Öskü (rural) + Szentgál (rural)

Masks: non-hostile - C; hostile - D; unfamiliar - B

time\date	2012-01-16	2012-01-17	2012-01-18	2012-01-19	2012-01-20
8:30	hostile	non-hostile	non-hostile	hostile	unfamiliar
10:30	non-hostile	hostile	non-hostile	non-hostile	non-hostile
12:30	non-hostile	non-hostile	hostile		hostile
14:30	hostile	hostile	hostile		

Cohort 3: Dunaújváros (urban) + Székesfehérvár (urban)

Masks: non-hostile - A; hostile - C; unfamiliar - B

time\date	2012-01-23	2012-01-24	2012-01-25	2012-01-26	2012-01-27
8:30	hostile	non-hostile	non-hostile	hostile	unfamiliar
10:30	non-hostile	hostile	hostile	non-hostile	non-hostile
12:30	non-hostile	non-hostile	hostile		hostile
14:30	hostile	hostile	non-hostile		

Cohort 4: Bánd (rural) + Salföld (rural)

Masks: non-hostile - B; hostile - D; unfamiliar - A

time\date	2012-01-30	2012-01-31	2012-02-01	2012-02-02	2012-02-03
8:30	hostile	non-hostile	non-hostile	hostile	non-hostile
10:30	non-hostile	hostile	hostile	non-hostile	unfamiliar
12:30	hostile	hostile	hostile		hostile
14:30	non-hostile	non-hostile	non-hostile		

Cohort 5: Siófok (urban) + Balatonfüred (urban)

Masks: non-hostile - B; hostile - C; unfamiliar - D

time\date	2012-02-20	2012-02-21	2012-02-22	2012-02-23	2012-02-24
8:30	non-hostile	hostile	hostile	hostile	non-hostile
10:30	hostile	non-hostile	hostile	non-hostile	unfamiliar
12:30	non-hostile	hostile	non-hostile		hostile
14:30	hostile	non-hostile	non-hostile		

Cohort 6: Babat (rural) + Üllő, Dóramajor (rural)

Masks: non-hostile - D; hostile - C; unfamiliar - A

time\date	2012-02-27	2012-02-28	2012-02-29	2012-03-01	2012-03-02
8:30	non-hostile	non-hostile	hostile	non-hostile	non-hostile
10:30	non-hostile	hostile	non-hostile	hostile	hostile
12:30	hostile	non-hostile	non-hostile		unfamiliar
14:30	hostile	hostile	hostile		

Cohort 7: Budapest, district 9-10 (urban) + district 11 (urban)

Masks: non-hostile - D; hostile - A; unfamiliar - B

time\date	2012-03-05	2012-03-06	2012-03-07	2012-03-08	2012-03-09
8:30	hostile	hostile	hostile	non-hostile	unfamiliar
10:30	non-hostile	non-hostile	non-hostile	hostile	hostile
12:30	hostile	non-hostile	hostile		non-hostile
14:30	non-hostile	hostile	non-hostile		

Cohort 8: Seregélyes-szőlőhegy (rural) + Szentgál (rural)

Masks: non-hostile - B; hostile - A; unfamiliar - C

time\date	2012-03-12	2012-03-13	2012-03-14	2012-03-15	2012-03-16
8:30	non-hostile	hostile	non-hostile	non-hostile	hostile
10:30	hostile	non-hostile	hostile	hostile	unfamiliar
12:30	non-hostile	hostile	non-hostile		non-hostile
14:30	hostile	non-hostile	hostile		

APPENDICES TO CHAPTER 5

Table A5.1: *Analysis of deviance tables of the full models with all considered confounding variables.*

A) Responses to human disturbance - return latencies (corresponding to Table 5.1A)

Dependent variables	χ^2	*df*	***P***
Intercept	0.139	1	0.710
Site	12.891	3	0.005
Phase	1.263	1	0.261
Nest height	1.585	1	0.208
Trapping status	7.913	1	0.005
Period length	1.025	1	0.311
Nestling number	4.679	1	0.031
Nestling age	0.144	1	0.705
Sex	1.028	1	0.311
Calendar date	0.000	1	0.986
Time of the day	3.048	1	0.081
Nest checks	0.053	1	0.818
Site × Phase	1.366	3	0.713

B) Responses to human disturbance – numbers of nest visits (corresponding to Table 5.1B)

Dependent variables	χ^2	*df*	***P***
Intercept	0.226	1	0.635
Site	8.232	3	0.041
Phase	0.533	1	0.466
Nest height	1.626	1	0.202
Trapping status	14.493	1	0.000
Period length	0.156	1	0.693
Nestling number	3.348	1	0.067
Nestling age	0.436	1	0.509
Sex	0.934	1	0.334
Calendar date	0.001	1	0.972
Time of the day	0.300	1	0.584
Nest checks	0.371	1	0.543
Site × Phase	0.268	3	0.966

C) Responses to hostile versus unfamiliar humans – return latencies (corresponding to Table 5.2A)

Dependent variables	χ^2	*df*	*P*
Site	22.184	3	<0.001
Person	0.161	1	0.689
Phase	0.992	1	0.319
Nest height	0.353	1	0.552
Sex	1.924	1	0.165
Trapping status	5.265	1	0.022
Nestling number	7.630	1	0.006
Nestling age	0.206	1	0.650
Period length	0.581	1	0.446
Pre-test latency	0.081	1	0.775
Baseline latency	3.995	1	0.046
Calendar date	0.155	1	0.693
Time of the day	1.418	1	0.234
Nest checks	0.012	1	0.911
Site × Person	2.481	3	0.479
Site × Phase	2.395	3	0.495
Person × Phase	0.038	1	0.845
Person × Trapped	0.203	1	0.653
Site × Person × Phase	6.712	3	0.082

D) Responses to hostile versus unfamiliar humans – numbers of nest visits (corresponding to Table 5.2B)

Dependent variables	χ^2	*df*	*P*
Intercept	0.040	1	0.841
Site	13.631	3	0.003
Person	0.001	1	0.973
Phase	0.227	1	0.634
Nest height	0.082	1	0.774
Sex	0.805	1	0.370
Trapping status	5.689	1	0.017
Nestling number	2.526	1	0.112
Nestling age	0.527	1	0.468
Period length	0.365	1	0.545
Pre-test nest visit number	1.477	1	0.224
Baseline nest visit number	16.347	1	0.000
Calendar date	0.108	1	0.742
Time of the day	1.836	1	0.175
Nest checks	0.335	1	0.563
Site × Person	1.801	3	0.615
Site × Phase	0.281	3	0.964
Person × Phase	0.007	1	0.934
Person × Trapped	0.082	1	0.775
Site × Person × Phase	2.015	3	0.569

E) Response to sparrowhawk – return latencies (corresponding to Table 5.3A)

Dependent variables	χ^2	***df***	***P***
Site	10.127		0.018
Stimulus	20.403		0.000
Nest height	0.079		0.778
Sex	0.767		0.381
Trapping status	0.819		0.365
Nestling number	3.654		0.056
Nestling age	0.223		0.637
Period length	1.186		0.276
Pre-test latency	1.140		0.286
Baseline latency	0.668		0.414
Calendar date	2.981		0.084
Time of the day	2.405		0.121
Site × Stimulus	7.465		0.058

F) Response to sparrowhawk – numbers of nest visits (corresponding to Table 5.3B)

Dependent variables	χ^2	***df***	***P***
Intercept	0.826	1	0.363
Site	14.037	3	0.003
Stimulus	30.836	1	0.000
Nest height	0.553	1	0.457
Sex	0.949	1	0.330
Trapping status	0.973	1	0.324
Nestling number	3.161	1	0.075
Nestling age	0.723	1	0.395
Period length	0.089	1	0.766
Pre-test nest visit number	0.185	1	0.667
Baseline nest visit number	10.953	1	0.001
Calendar date	1.671	1	0.196
Time of the day	3.903	1	0.048
Site × Stimulus	7.775	3	0.051

G) Correlation between response to humans and sparrowhawk – return latencies (corresponding to Table 5.4A)

Dependent variables	χ^2	***df***	***P***
Intercept	0.244	1	0.622
Sparrowhawk response	0.420	1	0.517
Site	3.875	3	0.276
Trapping status	4.075	1	0.044
Nest height	0.497	1	0.481
Nestling number	0.303	1	0.582
Nestling age	0.129	1	0.720
Phase	0.071	1	0.791
Period length	0.010	1	0.921
Sex	1.742	1	0.187
Site × Sparrowhawk response	0.545	3	0.909

H) Correlation between response to humans and sparrowhawk – numbers of nest visits (corresponding to Table 5.4B)

Dependent variables	χ^2	*df*	*P*
Intercept	1.912	1	0.167
Sparrowhawk response	0.346	1	0.557
Site	5.214	3	0.157
Trapping status	6.134	1	0.013
Nest height	1.436	1	0.231
Nestling number	1.844	1	0.175
Nestling age	0.701	1	0.402
Phase	0.045	1	0.832
Period length	0.041	1	0.840
Sex	2.059	1	0.151
Site × Sparrowhawk response	1.561	3	0.668

Table A5.2: *The phase × person interaction in the human disturbance test: A) least-squares means of the return latencies (logits of hazard ratios from Cox models; larger values represent shorter latencies), and B) pairwise differences (linear contrasts) among the combinations of phase order (first or second) and person (familiar or unfamiliar). P-values were adjusted with the Tukey method. See also Figure A5.3.*

A)

Person-Phase	Least-square mean ± *SE*	Confidence interval
Unfamiliar-First	-0.177 ± 0.220	-0.609 – 0.255
Familiar-First	-0.539 ± 0.262	-1.053 – -0.026
Unfamiliar-Second	-0.653 ± 0.265	-1.173 – -0.134
Familiar-Second	0.238 ± 0.218	-0.190 – 0.665

B)

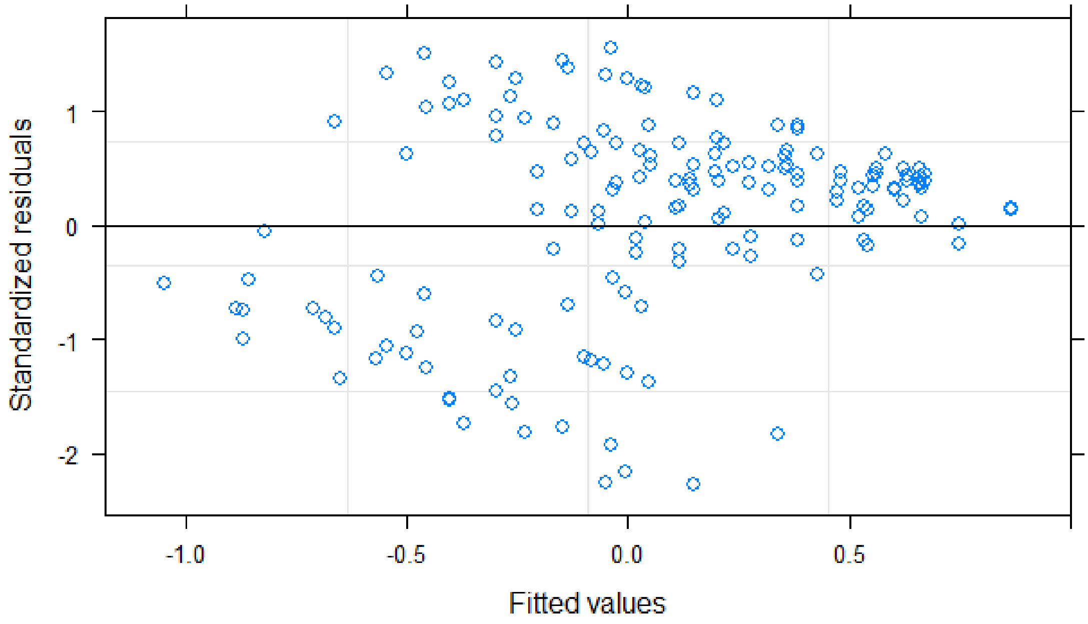
Contrast	Estimate ± *SE*	*z*	*P*
Unfamiliar-First – Familiar-First	0.363 ± 0.390	0.93	0.789
Unfamiliar-First – Unfamiliar-Second	0.477 ± 0.388	1.23	0.609
Unfamiliar-First – Familiar-Second	-0.414 ± 0.267	-1.55	0.406
Familiar-First – Unfamiliar-Second	0.114 ± 0.297	0.38	0.981
Familiar-First – Familiar-Second	-0.777 ± 0.386	-2.01	0.183
Unfamiliar-Second – Familiar-Second	-0.891 ± 0.385	-2.32	0.094

Table A5.3: *Linear contrasts between urban and rural habitats in the dove phase and sparrowhawk phase.*

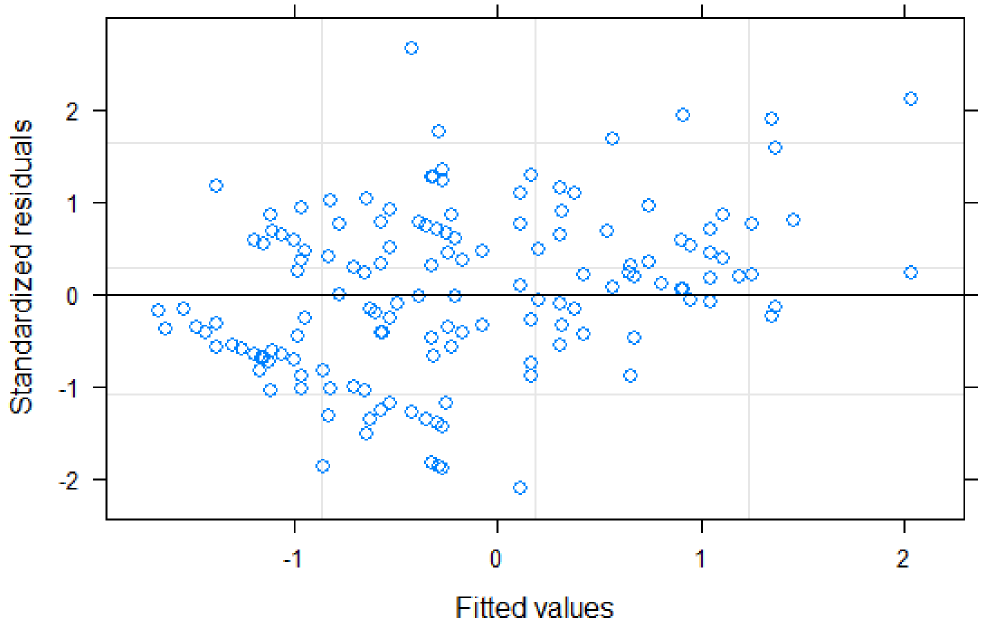
Response variable	Phase	Urban-rural contrast ± *SE*	*z*	*P*
Return latency	Dove	0.951 ± 0.525	1.812	0.070
	Sparrowhawk	1.990 ± 0.583	3.414	0.001
Number of nest visits	Dove	0.543 ± 0.376	1.444	0.157
	Sparrowhawk	1.363 ± 0.481	2.833	0.007

Figure A5.1: *Model diagnostic plots. As it was not possible to create model diagnostic plots for our Cox mixed-effects models with the* coxme *package, Figures C and E were created from Cox proportional hazard ratio models with the same fixed factor structure, but without random factors.*

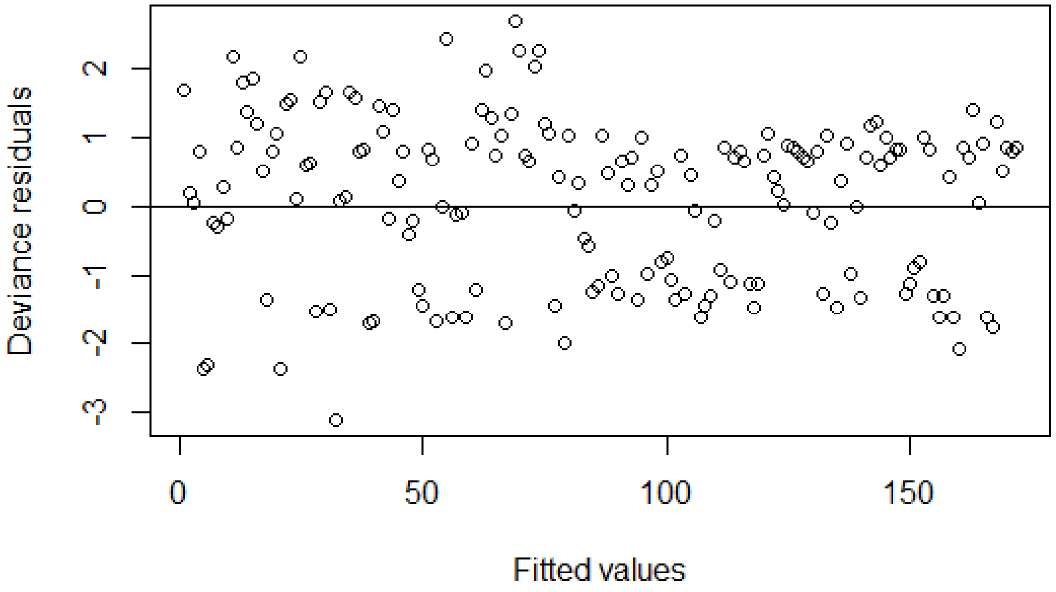
A) Responses to human disturbance - return latencies (corresponding to Table 5.1A)



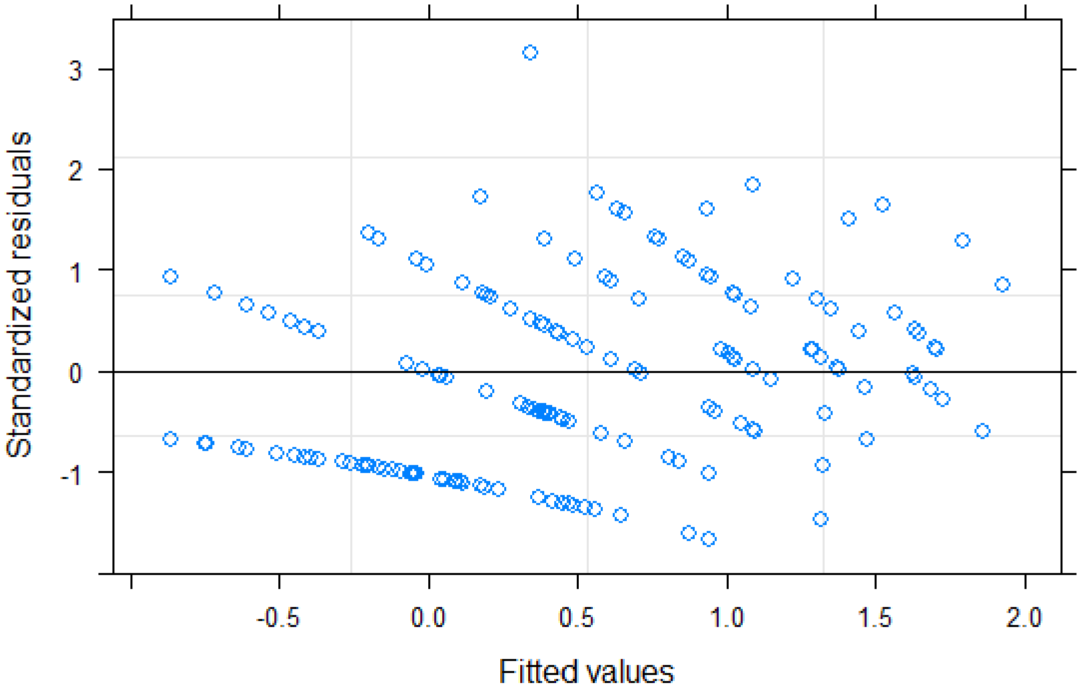
B) Responses to human disturbance – numbers of nest visits (corresponding to Table 5.1B)



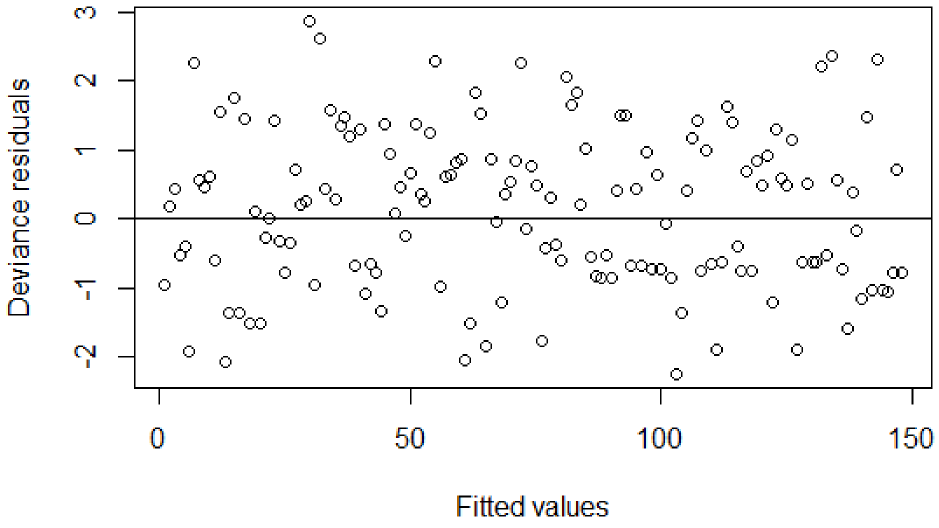
C) Responses to hostile versus unfamiliar humans – return latencies (corresponding to Table 5.2A)



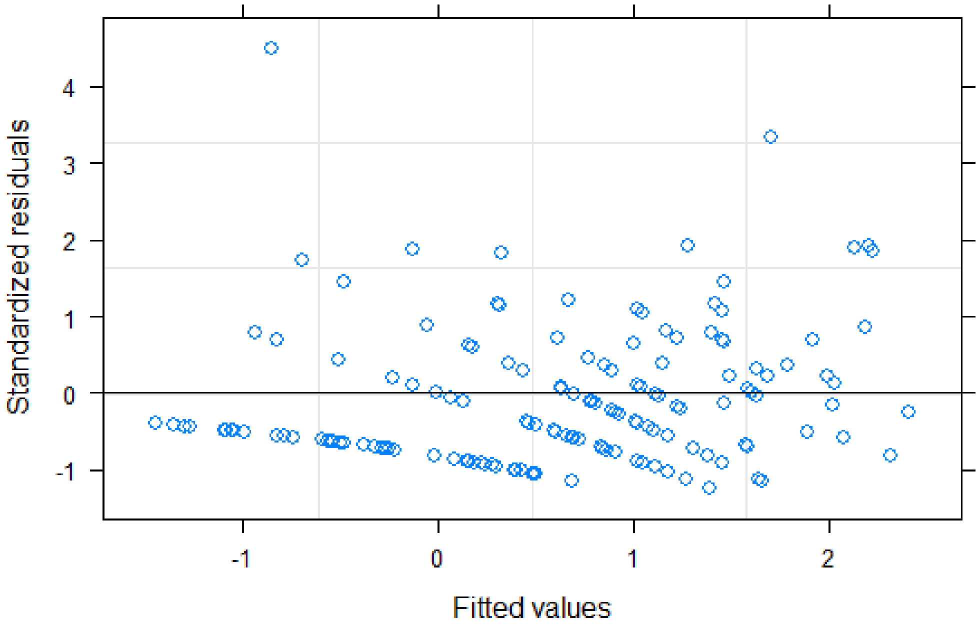
D) Responses to hostile versus unfamiliar humans – numbers of nest visits (corresponding to Table 5.2B)



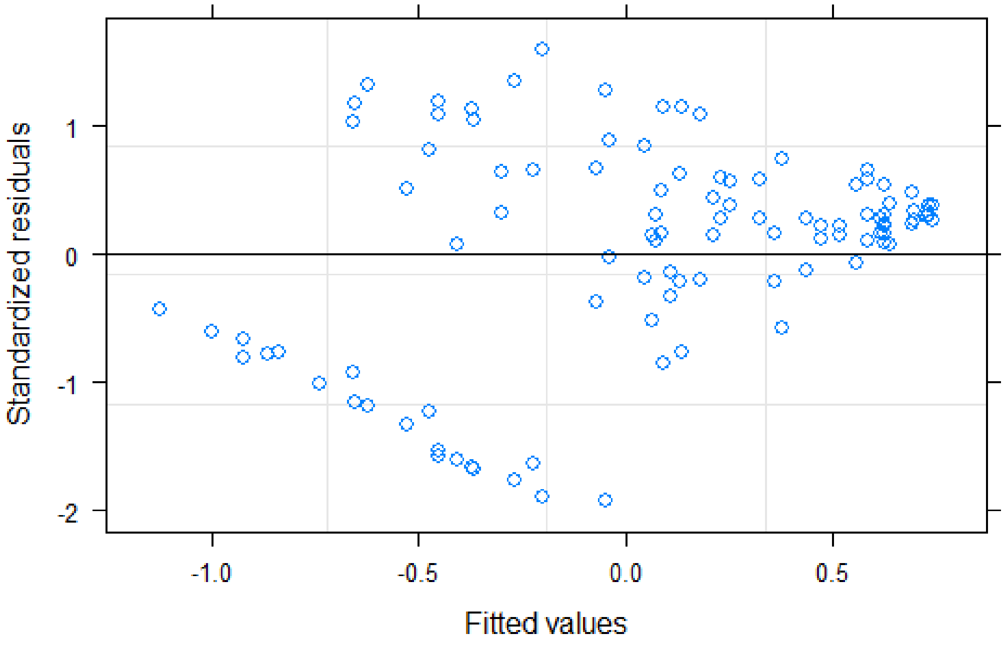
E) Response to sparrowhawk – return latencies (corresponding to Table 5.3A)



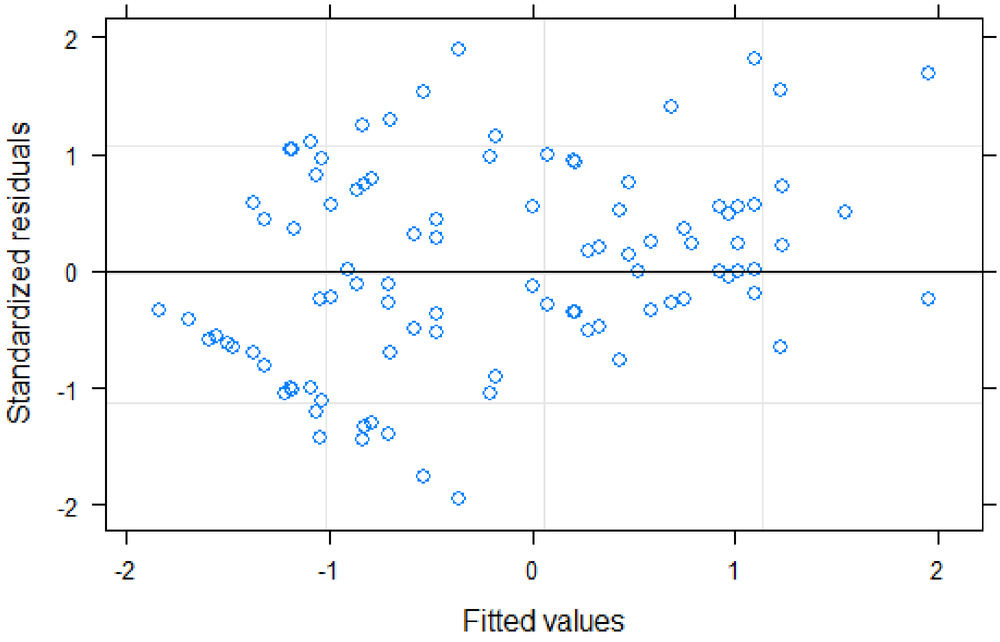
F) Response to sparrowhawk – numbers of nest visits (corresponding to Table 5.3B)



G) Correlation between response to humans and sparrowhawk – return latencies (corresponding to Table 5.4A)



H) Correlation between response to humans and sparrowhawk – numbers of nest visits (corresponding to Table 5.4B)



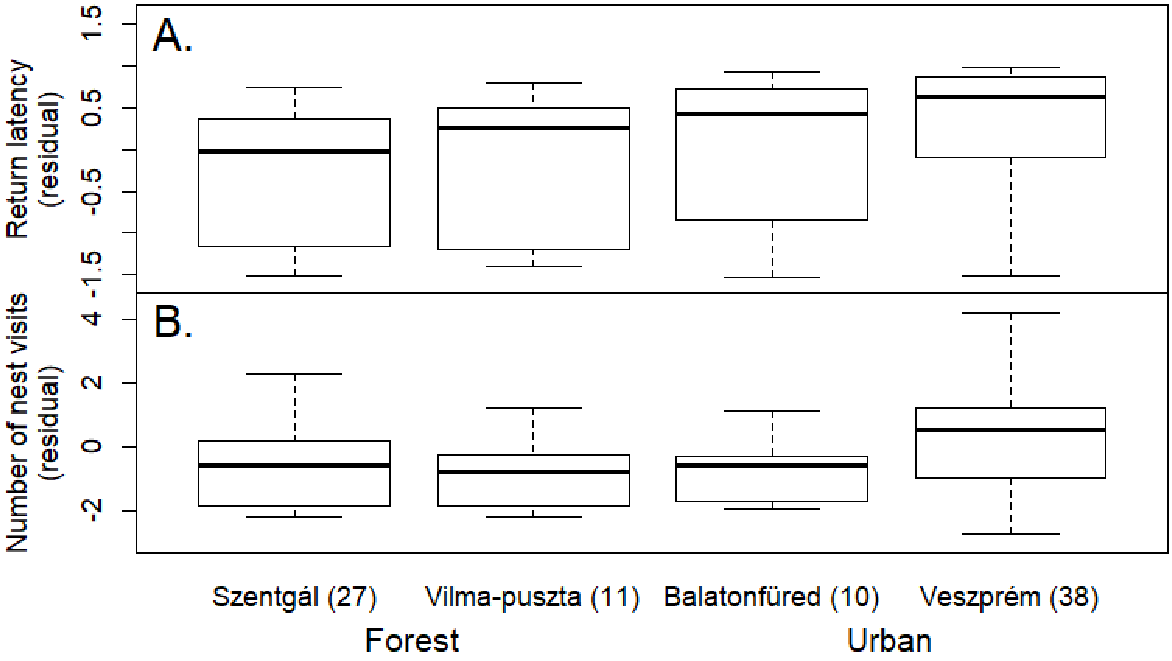


Figure A5.2: *Residual return latencies (A) and residual numbers of nest visits (B) in the human disturbance test.*

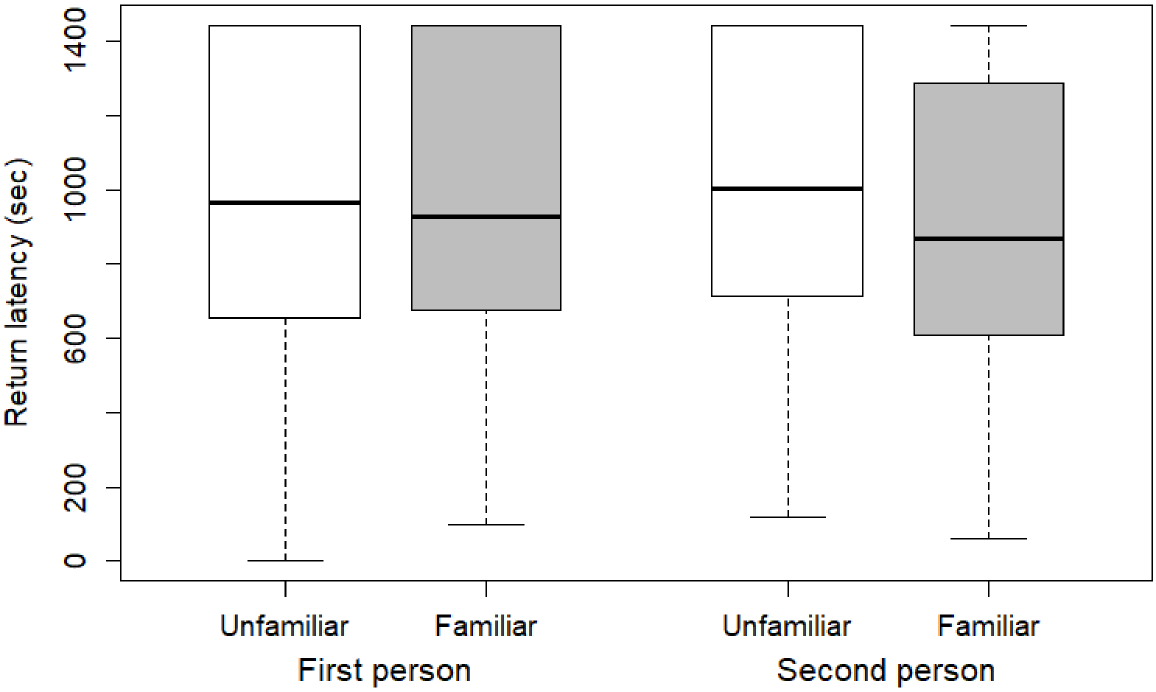


Figure A5.3: *Return latencies in the human disturbance test, showing the person × phase interaction*

APPENDICES TO CHAPTER 6

Table A6.1. *Contingency table of papers initially considered by the 2 independent observers as potentially meeting (YES) or certainly not meeting (NO) the criteria for inclusion based on paper title and abstract. "Single-screened" papers were assessed only by 1 of the search engines and thus screened only by 1 of the observers (201 out of 406 papers).*

Inclusion decision	**Observer 1 – YES**	**Observer 1 - NO**	**Single-screened**
Observer 2 - YES	56	31	29
Observer 2 - NO	6	112	40
Single-screened	12	120	-

Table A6.2. *Contingency table of urbanization scores given by the 2 observers (columns: EV, rows: GS) for each site in each study. Between-observer repeatability r = 0.982 (Spearman rank correlation).*

Score	**1**	**2**	**3**	**4**	**5**
1	39	0	0	0	0
2	2	30	0	0	0
3	0	2	29	4	0
4	0	0	1	34	1
5	0	0	0	2	17

Table A6.3. *Papers excluded from meta-analysis based on full-text screening, grouped by reason for exclusion. N: Number of papers excluded for each particular reason.*

Reason for exclusion	***N***	**References**
No gradient defined for urbanization (all sites on the same urbanization level)	31	Balogh et al., 2011; Baudains and Lloyd, 2007; Becker and Weisberg, 2015; Bonnington et al., 2013, 2015; Cox et al., 2013; DeGregorio et al., 2014; Eguchi and Takeishi, 1997; Engel et al., 1988; Francis et al., 2009; Górski and Antczak, 1999; Grégoire et al., 2003; Groom, 1993; Guerena et al., 2014; Guerrieri and Santucci, 1996; Jedraszko-Dabrowska, 1990; Kurucz et al., 2010, 2012, 2015; Langston et al., 2007; Major et al., 1996; Meckstroth and Miles, 2005; Møller, 2010; Morgan et al., 2011; ÓhUallacháin, 2014; Pescador and Peris, 2007; Rees et al., 2014; Robertson, 1990; Spohr et al., 2004; Stirnemann et al., 2015; Wong et al., 1998
Gradient only for non-urban (rural) anthropogenic disturbance	4	Borges and Marini, 2009; Marzluff and Neatherlin, 2006; Mezquida et al., 2004; Vierling, 2000
Nest survival not investigated (presence/absence of species, adult survival or individual offspring survival)	8	Arrowood et al., 2001; Bonnington et al., 2014; Brown and Graham, 2015; Chang and Lee, 2015; Chiron and Julliard, 2007; Cordero and Rodriguez-Teijeiro, 1990; Hedblom and Söderström, 2011; Long and Long, 1992
Nest survival – urbanization relationship not tested	6	Hadad et al., 2015; Marzluff et al., 2007; Miller et al., 2015; Sedláček and Fuchs, 2008; Sethi et al., 2011; Stout et al., 2007
Only daily nest survival reported (cannot be converted to overall survival rates)	7	Donnelly and Marzluff, 2004; Hušek et al., 2010; Morrison and Bolger, 2002; Phillips et al., 2005; Rodewald et al., 2013; Stracey, 2011; Stracey and Robinson, 2012b
Only multivariate models reported	18	Ali Chokri and Selmi, 2011; Blair, 2004; Burhans and Thompson, 2006; Buxton and Benson, 2015; Cervantes-Cornihs et al., 2009; Friesen et al., 2013; Haskell et al., 2001; Meffert et al., 2012; Mikula et al., 2014; Patterson et al., 2016; Reidy et al., 2009; Rivera-López and Macgregor-Fors, 2016; Schlossberg et al., 2011; Shipley et al., 2013; Stracey and Robinson, 2012a; Sumasgutner et al., 2014; Suvorov and Šálek, 2013; Tarvin and Smith, 1995
Data overlapping with another study	13	Bakermans and Rodewald, 2006; Borgmann and Rodewald, 2004; Leston and Rodewald, 2006; Piper and Catterall, 2006; Rodewald et al., 2015, 2011a, 2011b, 2014; Rodewald and Kearns, 2011; Rodewald and Shustack, 2008a, 2008b, Shustack and Rodewald, 2010, 2011

***Table A6.4**. Summary of the papers included in the meta-analysis. k – Number of effect sizes per study. NA – Not applicable due to artificial nests being used in the study.*

Reference	**Species latin name**	**Nest type**	***k***	**Data source**	**Continent**
Lin et al., 2015	*Accipiter trivirgatus*	natural	1	numbers (reported)	Asia
Kuranov, 2008	*Acrocephalus dumetorum*	natural	1	numbers (reported)	Europe
Grandmaison and Niemi, 2007	*Agelaius phoeniceus*	natural	1	numbers (reported)	North America
Bowman and Woolfenden, 2001	*Aphelocoma coerulescens*	natural	6	percentage (reported)	North America
Vennesland and Butler, 2004	*Ardea herodias*	natural	2	percentage (from author)	North America
England et al., 1995	*Buteo swainsoni*	natural	5	numbers (reported)	North America
Kosiński, 2001	*Carduelis chloris*	natural	1	percentage (reported)	Europe
Patten and Bolger, 2003	*Aimophila ruficeps, Chamaea fasciata, Pipillio crissalis, Pipillio maculatus*	natural	4	numbers (from author)	North America
Beck and Heinsohn, 2006	*Corcorax melanorhamphos*	natural	1	numbers (reported)	Australia
Brahmia et al., 2013	*Cyanistes caeruleus*	natural	3	numbers (from author)	Africa
Vigallon and Marzluff, 2005	*Cyanocitta stelleri*	natural	1	numbers (reported)	North America
Reidy et al., 2008	*Dendroica chrysoparia*	natural	1	numbers (reported)	North America
Cempulik, 1993	*Gallinula chloropus*	natural	1	numbers (from author)	Europe
Newell and Kostalos, 2007	*Hylocichla mustelina*	natural	1	daily predation rates	North America
Pretelli et al., 2015	*Hymenops perspicillatus, Pseudoliestes virescens*	natural	2	numbers (reported)	South America
Mazumdar and Kumar, 2014	*Nectarinia asiatica*	natural	1	numbers (reported)	Asia
Eden, 1985	*Pica pica*	natural	1	numbers (reported)	Europe
Antonov and Atanasova, 2003	*Pica pica*	natural	1	numbers (reported)	Europe
Sachteleben et al., 1992	*Pica pica*	natural	1	percentage (reported)	Europe
Morimoto et al., 2012	*Seiurus aurocapilla*	natural	1	percentage (reported)	North America
Misztal et al., 2008	*Sitta europaea*	natural	1	numbers (reported)	Europe
Solonen and Ursin, 2008	*Strix aluco*	natural	10	numbers (from author)	Europe
Kuranov, 2009	*Ficedula hypoleuca, Sturnus vulgaris, Parus*	natural	4	percentage (reported)	Asia

	major, Phoenicurus phoenicurus				
Newhouse et al., 2008	*Troglodytes aedon*	natural	1	numbers (reported)	North America
Hofer et al., 2010	*Troglodytes aedon*	natural	1	numbers (reported)	North America
Ibáñez-Álamo and Soler, 2010	*Turdus merula*	natural	1	percentage (reported)	Europe
Vogrin, 2000	*Turdus merula*	natural	1	numbers (reported)	Australia
Kentish et al., 1995	*Turdus merula*	natural	1	percentage (reported)	Europe
Cardilini et al., 2013	*Vanellus miles*	natural	1	numbers (reported)	Australia
Kamp et al., 2014	*Vanellus vanellus*	natural	1	numbers (reported)	Europe
Thorington and Bowman, 2003	NA	artificial	1	percentage (reported)	North America
Gering and Blair, 1999	NA	artificial	4	figure	North America
Wilcove, 1985	NA	artificial	1	percentage (reported)	North America
van Heezik et al., 2008	NA	artificial	1	percentage (reported)	New Zealand
López-Flores et al., 2009	NA	artificial	1	numbers (reported)	Central America
Ryder et al., 2010	NA	artificial	1	percentage (reported)	North America
Jokimäki and Huhta, 2000	NA	artificial	4	percentage (reported)	Europe
Melampy et al., 1999	NA	artificial	2	percentage (reported)	North America
Danielson et al., 1997	NA	artificial	1	percentage (reported)	North America
Jobin and Picman, 1997	NA	artificial	2	percentage (reported)	North America
Jobin and Picman, 2002	NA	artificial	2	percentage (reported)	North America
Jokimäki et al., 2005	NA	artificial	3	numbers (reported)	Europe
Latta et al., 2012	NA	artificial	1	numbers (reported)	North America
Sasvári et al., 1995	NA	artificial	18	figure	Europe
Piper and Catterall, 2004	NA	artificial	6	percentage (reported)	Australia
Piper et al., 2002	NA	artificial	1	percentage (reported)	Australia
De Santo and Willson, 2001	NA	artificial	2	figure	North America
Keyser, 2002	NA	artificial	4	numbers (reported)	North America
Matthews et al., 1999	NA	artificial	2	percentage (reported)	Australia
Lumpkin et al., 2012	NA	artificial	1	coefficient	North America
Czyzowski et al., 2006	NA	artificial	1	numbers (reported)	Europe

Table A6.5. *Comparison of the characteristics of the artificial nests data subset and natural nests data subset.*

	Artificial nests Median (Mean ± *SD*) [Frequencies for factors]	**Natural nests** Median (Mean ± *SD*)	**Difference artificial-natural nests**
Min urbanization score	1 (1.4 ± 0.8)	2 (1.6 ± 0.5)	$t = -2.54$, $df = 115$, $P = 0.012$
(1 / 2 / 3 / 4)	(49 /6 / 2 / 2)	(28 / 27 / 2/ 1)	$\chi^2 = 19.42$, $df = 3$, $P < 0.001$
Max urbanization score	3 (3.8 ± 0.9)	4 (3.8 ± 0.4)	$t = -2.96$, $df = 115$, $P = 0.004$
(3 / 4 / 5)	(42/ 4 / 13)	(16 / 30 / 12)	$\chi^2 = 31.57$, $df = 2$, $P < 0.001$
Predation as only source of mortality (yes / no)	[59 / 0]	[20 / 38]	$\chi^2 = 54.30$, $df = 1$, $P < 0.001$
Predation scoring (partial / complete / 1 egg)	[50 / 0 / 9]	[2 / 56 / 0]	$\chi^2 = 109.31$, $df = 2$, $P < 0.001$
Nest openness (cup / hole / orb)	[53 / 6 / 0]	[36 / 20 / 2]	$\chi^2 = 12.78$, $df = 2$, $P = 0.002$
Nest position (elevated / ground / mix)	[26 / 28 / 5]	[51 / 6 / 1]	$\chi^2 = 25.01$, $df = 2$, $P < 0.001$
Nest height above ground [m]	0 (0.8 ± 1.0)	2.8 (2.2 ± 2.2)	$t = -4.94$, $df = 84$, $P < 0.001$
Egg number	2 (2.2 ± 1.0)	3.8 (4.2 ± 1.2)	$t = -5.79$, $df = 98$, $P < 0.001$
Number of nests	105 (200.4 ± 231.3)	87 (207.6 ± 258.3)	$t = -0.02$, $df = 113$, $P = 0.987$
Study duration [days]	12 (12.2 ± 5.9)	28 (41.2 ± 21.1)	$t = -7.72$, $df = 64$, $P < 0.001$
Median study year	1997 (1997.8 ± 5.8)	2004 (2000.5 ± 15.0)	$t = -2.26$, $df = 115$, $P = 0.025$
Publication year	2002 (2002.2 ± 4.9)	2008 (2007.8 ± 7.8)	$t = -4.78$, $df = 115$, $P < 0.001$
Number of ES	59	58	
Number of species	0	32	

Table A6.6. Parameter estimates for the meta-analytic and meta-regression models run on full data set. *Effect size presented is r. M – mean estimate, CI.lb – lower bound for the 95% Confidence Interval, CI.ub – upper bound for the 95% Confidence Interval, I^2_{total} – total heterogeneity. Effect size used is Zr. Stars indicate point estimates that are significantly different from zero (95% Confidence Intervals not crossing zero).*

Model	***M***	***CI.lb***	***CI.ub***	I^2_{total}
Meta-analytic mean – all data	-0.003	-0.080	0.074	92.7%
Artificial vs. Natural nests:				
Artificial nests *	-0.116	-0.224	-0.005	
Natural nests	0.081	-0.015	0.176	
Difference: Artificial **-** Natural nests *	0.195	0.050	0.332	

Table A6.7. Parameter estimates for the meta-regression models for data from the artificial nests data subset. *Effect size presented is r. M – mean estimate, CI.lb – lower bound for the 95% Confidence Interval, CI.ub – upper bound for the 95% Confidence Interval, I^2_{total} – total heterogeneity. Stars indicate point estimates that are significantly different from zero (95% Confidence Intervals not crossing zero).*

Model	***M***	***CI.lb***	***CI.ub***	I^2_{total}
Meta-analytic mean – artificial nests	-0.118	-0.238	0.006	93.1%
Nest openness:				
Cup	-0.119	-0.239	0.004	
Hole	-0.036	-0.214	0.144	
Nest position:				
Elevated	-0.087	-0.221	0.050	
Ground	-0.130	-0.258	0.003	
Mix	-0.157	-0.333	0.028	
Egg number (slope)	-0.006	-0.131	0.119	
Study duration [days] (slope)	-0.073	-0.202	0.059	
Median study year (slope)	-0.041	-0.141	0.060	
Publication year (slope)	-0.016	-0.120	0.088	
Min urbanization score:				
1	-0.115	-0.273	0.049	
2	-0.176	-0.435	0.110	
3	-0.071	-0.477	0.359	
4	0.190	-0.143	0.485	
Max urbanization score:				
3	-0.103	-0.259	0.058	
4 *	-0.312	-0.557	-0.017	
5	-0.014	-0.262	0.236	

Table A6.8. Parameter estimates for the phylogenetic meta-regression models for data from the natural nests data subset. *Effect size presented is r. M – mean estimate, CI.lb – lower bound for the 95% Confidence Interval, CI.ub – upper bound for the 95% Confidence Interval,* I^2_{total} *– total heterogeneity. Stars indicate point estimates that are significantly different from zero (95% Confidence Intervals not crossing zero). Univariate meta-regressions control for shared evolutionary history of the species (i.e. phylogenetic meta-regression was used).*

Model	***M***	***CI.lb***	***CI.ub***	I^2_{total}
Meta-analytic mean	0.079	-0.007	0.165	90.0%
Phylogenetic meta-analytic mean	0.034	-0.163	0.228	91.5%
Phylogeny				78.5%
Predation as only source of mortality:				
No	-0.020	-0.192	0.153	
Yes	0.107	-0.067	0.276	
Nest openness:				
Cup	0.019	-0.169	0.205	
Hole	0.131	-0.118	0.364	
Orb	-0.162	-0.462	0.172	
Nest position:				
Elevated	0.001	-0.202	0.204	
Ground	0.147	-0.114	0.389	
Mix	-0.041	-0.472	0.405	
Nest height above ground [m] (slope)	-0.091	-0.197	0.018	
Egg number (slope)	0.043	-0.046	0.131	
Study duration [days] (slope)	0.037	-0.190	0.260	
Median study year (slope)	0.041	-0.014	0.096	
Publication year (slope)	0.027	-0.040	0.094	
Min urbanization score:				
1	0.056	-0.194	0.299	
2	0.029	-0.192	0.247	
3	-0.105	-0.467	0.286	
4	0.181	-0.283	0.577	
Max urbanization score:				
3	0.088	-0.141	0.307	
4	-0.016	-0.246	0.215	
5	0.005	-0.231	0.240	

Table A6.9. Parameter estimates for the meta-regression model for the natural nests data subset with species identity used as a predictor. *Effect size presented is r. M – mean estimate, CI.lb – lower bound for the 95% Confidence Interval, CI.ub – upper bound for the 95% Confidence Interval. Stars indicate point estimates that are significantly different from zero (95% Confidence Intervals not crossing zero).*

Model	***M***	***CI.lb***	***CI.ub***
Species:			
*Accipiter trivirgatus **	0.397	0.154	0.596
Acrocephalus dumetorum	0.074	-0.115	0.259
Agelaius phoeniceus	-0.231	-0.413	-0.033
Aimophila ruficeps	0.139	-0.263	0.499
Aphelocoma coerulescens	-0.041	-0.143	0.062
*Ardea herodias **	-0.238	-0.356	-0.113
*Buteo swainsoni **	-0.123	-0.231	-0.012
Carduelis chloris	0.153	-0.052	0.346
Chamaea fasciata	0.220	-0.061	0.469
*Corcorax melanorhamphos **	-0.269	-0.486	-0.020
*Cyanistes caeruleus **	0.310	0.074	0.512
*Cyanocitta stelleri **	-0.791	-0.956	-0.249
Dendroica chrysoparia	0.070	-0.154	0.287
Ficedula hypoleuca	0.128	-0.059	0.306
Gallinula chloropus	0.044	-0.185	0.268
Hylocichla mustelina	0.059	-0.186	0.297
Hymenops perspicillatus	-0.029	-0.288	0.234
Nectarinia asiatica	-0.112	-0.319	0.106
Parus major	0.167	-0.074	0.389
*Phoenicurus phoenicurus **	0.267	0.058	0.452
*Pica pica **	0.179	0.042	0.310
Pipilo crissalis	-0.082	-0.321	0.167
*Pipilo maculatus **	0.355	0.022	0.617
Pseudoleistes virescens	-0.134	-0.406	0.160
Seiurus aurocapilla	-0.152	-0.376	0.089
Sitta europaea	-0.043	-0.311	0.231
*Strix aluco **	-0.147	-0.268	-0.022
Sturnus vulgaris	0.035	-0.165	0.233
*Troglodytes aedon **	0.572	0.411	0.699
*Turdus merula **	0.202	0.076	0.321
Vanellus miles	0.365	-0.021	0.656
*Vanellus vanellus **	0.365	0.106	0.577

Table A6.10. Sensitivity analysis using alternative urbanization scores for the study sites: Parameter estimates for the meta-analytic and meta-regression models run on full data set. *Effect size presented is r. M – mean estimate, CI.lb – lower bound for the 95% Confidence Interval, CI.ub – upper bound for the 95% Confidence Interval,* I^2_{total} *– total heterogeneity. Effect size used is Zr. Stars indicate point estimates that are significantly different from zero (95% Confidence Intervals not crossing zero).*

Model	***M***	***CI.lb***	***CI.ub***	I^2_{total}
Meta-analytic mean – all data	-0.007	-0.085	0.071	92.8%
Artificial vs. Natural nests:				
Artificial nests *	-0.123	-0.232	-0.012	
Natural nests	0.080	-0.017	0.175	
Difference: Artificial - Natural nests *	0.201	0.056	0.338	

Table A6.11. Sensitivity analysis using alternative urbanization scores for the study sites: Parameter estimates for the meta-regression models for data from the artificial nests data subset. *Effect size presented is r. M – mean estimate, CI.lb – lower bound for the 95% Confidence Interval, CI.ub – upper bound for the 95% Confidence Interval,* I^2_{total} *– total heterogeneity. Stars indicate point estimates that are significantly different from zero (95% Confidence Intervals not crossing zero).*

Model	***M***	***CI.lb***	***CI.ub***	I^2_{total}
Meta-analytic mean – artificial nests	-0.125	-0.245	-0.002	92.4%
Nest openness:				
Cup	-0.126	-0.246	-0.003	
Hole	-0.046	-0.218	0.129	
Nest position:				
Elevated	-0.096	-0.228	0.040	
Ground	-0.137	-0.263	-0.005	
Mix	-0.161	-0.328	0.016	
Egg number (slope)	0.001	-0.124	0.126	
Study duration [days] (slope)	-0.079	-0.207	0.051	
Median study year (slope)	-0.042	-0.142	0.058	
Publication year (slope)	-0.017	-0.121	0.087	
Min urbanization score:				
1	-0.123	-0.281	0.041	
2	-0.172	-0.431	0.115	
3	-0.095	-0.495	0.337	
4	0.187	-0.137	0.476	
Max urbanization score:				
3	-0.103	-0.259	0.059	
4	-0.324	-0.566	-0.031	
5	-0.034	-0.282	0.217	

Table A6.12. Sensitivity analysis using alternative urbanization scores for the study sites: Parameter estimates for the phylogenetic meta-regression models for data from the natural nests data subset. *Effect size presented is r. M – mean estimate, CI.lb – lower bound for the 95% Confidence Interval, CI.ub – upper bound for the 95% Confidence Interval, I^2_{total} – total heterogeneity. Stars indicate point estimates that are significantly different from zero (95% Confidence Intervals not crossing zero).*

Model	***M***	***CI.lb***	***CI.ub***	I^2_{total}
Meta-analytic mean	0.079	-0.008	0.165	90.0%
Phylogenetic meta-analytic mean	0.045	-0.126	0.212	91.5%
Phylogeny				
Predation as only source of mortality:				
No	-0.016	-0.134	0.101	
Yes *	0.160	0.050	0.266	
Nest openness:				
Cup	0.059	-0.041	0.158	
Hole *	0.219	0.032	0.391	
Orb	-0.132	-0.431	0.195	
Nest position:				
Elevated	0.063	-0.034	0.158	
Ground	0.182	-0.019	0.368	
Mix	0.074	-0.379	0.499	
Nest height above ground [m] (slope)	-0.134	-0.261	-0.002	
Egg number (slope)	0.043	-0.046	0.131	
Study duration [days] (slope)	0.041	-0.182	0.261	
Median study year (slope)	0.060	-0.013	0.133	
Publication year (slope)	0.033	-0.047	0.112	
Min urbanization score:				
1	0.026	-0.192	0.242	
2	0.065	-0.117	0.243	
3	-0.088	-0.434	0.280	
4	0.127	-0.333	0.538	
Max urbanization score:				
3	0.146	-0.025	0.308	
4	0.058	-0.081	0.195	
5	0.048	-0.116	0.208	

Table A6.13. Sensitivity analysis using alternative urbanization scores for the study sites: Parameter estimates for the meta-regression model for the natural nests data subset with species identity used as a predictor. *Effect size presented is r. M – mean estimate, CI.lb – lower bound for the 95% Confidence Interval, CI.ub – upper bound for the 95% Confidence Interval. Stars indicate point estimates that are significantly different from zero (95% Confidence Intervals not crossing zero).*

Model	***M***	***CI.lb***	***CI.ub***
Species:			
Accipiter trivirgatus *	0.397	0.152	0.597
Acrocephalus dumetorum	0.074	-0.118	0.262
Agelaius phoeniceus	-0.203	-0.390	0.000
Aimophila ruficeps	0.201	-0.204	0.547
Aphelocoma coerulescens	-0.050	-0.153	0.054
Ardea herodias *	-0.238	-0.358	-0.110
Buteo swainsoni *	-0.123	-0.232	-0.011
Carduelis chloris	0.144	-0.064	0.340
Chamaea fasciata	0.121	-0.164	0.388
Corcorax melanorhamphos *	-0.269	-0.488	-0.018
Cyanistes caeruleus *	0.310	0.073	0.513
Cyanocitta stelleri *	-0.791	-0.956	-0.248
Dendroica chrysoparia	0.070	-0.156	0.290
Ficedula hypoleuca	0.128	-0.062	0.309
Gallinula chloropus	0.044	-0.188	0.270
Hylocichla mustelina	-0.009	-0.253	0.236
Hymenops perspicillatus	-0.029	-0.29	0.236
Nectarinia asiatica	-0.112	-0.322	0.109
Parus major	0.167	-0.076	0.391
Phoenicurus phoenicurus *	0.267	0.056	0.455
Pica pica *	0.179	0.040	0.311
Pipilo crissalis	0.135	-0.116	0.370
Pipilo maculatus *	0.357	0.023	0.619
Pseudoleistes virescens	-0.134	-0.407	0.162
Seiurus aurocapilla	-0.152	-0.379	0.091
Sitta europaea	-0.107	-0.370	0.172
Strix aluco *	-0.148	-0.269	-0.022
Sturnus vulgaris	0.035	-0.168	0.236
Troglodytes aedon *	0.572	0.410	0.700
Turdus merula *	0.201	0.074	0.322
Vanellus miles	0.365	-0.022	0.657
Vanellus vanellus *	0.365	0.104	0.578