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INDIVIDUAL AND POPULATION LEVEL EFFECTS OF URBANIZATION ON HOUSE SPARROWS *(PASSER DOMESTICUS)* IN HUNGARY

Ph.D. Thesis

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AZ URBANIZÁCIÓ EGYEDI ÉS POPULÁCIÓ SZINTŰ HATÁSAI A HÁZI VEREBEKNÉL *(PASSER DOMESTICUS)* MAGYARORSZÁGON

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Az értekezést bírálóként elfogadásra javaslom:

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ABSTRACT *(in English)*

Human activity has been transforming our planet's face for a long time, but the impact of urbanization on our environment has never been as intense as in the last few decades. Yet, our understanding on its effects on wildlife and on the changes it generates in ecological driving mechanisms is very scanty. This thesis investigates some of the population and individual level effects of urbanization on a typical human commensalist bird, the house sparrow *(Passer domesticus)*, which is perhaps the most familiar bird species in the world. We conducted indoor and outdoor experiments, breeding biology monitoring and intensive ringing and data collection along urban to rural habitat gradients and (i) assessed adult sparrows' body condition and health state, (ii) compared the reproductive success and nestling development in differently urbanized populations, (iii) assessed the relative importance of genetic and environmental factors during the chick-rearing period, (iv) also assessed urban and rural birds' perceived predation risk inferred from their risk-taking behavior and (v) introduced and validated a semi-automated method to quantify degree of habitat urbanization from land-cover characteristics. Our results suggest that, compared to their rural conspecifics, adult urban sparrows are smaller but do not show signs of elevated stress levels (i.e. they are not in inferior body condition). We also showed that sparrows in a more urbanized habitat suffer from higher rates of nestling mortality and also fledge significantly smaller young, probably because the nestling diet is of poorer quality in cities than in rural sites. We also found that urban adult sparrows responded more strongly to simulated predator attacks, implying higher predation risk in their habitats, at least posed by sparrowhawks. The combined results presented in this thesis provide insights into the effects of urbanization on the house sparrow, and along with the tool we proposed for quantifying urbanization it may contribute to the better understanding of the ecology of urban bird populations.

ABSTRACT *(auf Deutsch)*

In den letzen Jahrzehnten formen die Menschen das Bild der Erde immer schneller und intensiver um. Die Verstädterung – die Umgestaltung des natürlichen Lebensraums zur Städte – ist ein bedeutendes Teil von diesem Prozess. Gegen ihre Wichtigkeit sind die Wirkungen der Verstädterung auf das einzige Lebenswesen und auf die Populationen bestimmenden ökologischen Prozessen nicht befriedigend bekannt. Diese Dissertation prüft die Einzel- und Populationswirkungen der Urbanisation, ihre Modellrasse ist der Haussperling (*Passer domesticus*), der vielleicht die bekannteste Vogel an der ganze Welt infolge seines menschenfreundlichen Lebensstils ist. Während unserer Untersuchungen wurden in dem Freie und in der Gefangenschaft lebende Vögel nach den Urbanisationgradientverfahren beobachtet und geprüft und die Zuchtbiologie in mehreren Population gefolgt. Unsere Ziele waren (i) die Kondition der städtischen und ländlichen Vögel zu vergleichen, (ii) ihre reproduktive Erfolge und Zuchtentwicklung gegenüberzustellen, (iii) die Wichtigkeit der Umgebung in der Nachkommenerziehungssperiod zu messen, (iv) die Risikoübernahme der städtischen und ländlichen Vögel gegen Raubtiere zu vergleichen, (v) und ein Verfahren vorzustellen und überzuprüfen, mit dem man das Maß der Verstädterung aus Erdoberlächedaten ausrechnen kann. Laut unseren Ergebnissen sind die urbanisierten Vögel kleiner, aber sie zeigen keine Signale des verstärkten Stress. Wir haben auch nachgewiesen, dass die Nummer und die Größe der urbanisierten Jungvögel geringer als der ländlichen waren, wahrscheinlich wegen der schlechtere Nahrungsqualität im Frühperiod. Die Ergebnisse erweisen stärkere Nachwirkungen bei urbanisierten Vögeln während eines simulierten Sperberangriffs, aus denen wir darauf erschließen können, dass diese Vögel gegen einer größeren Räubertiergefahr in ihrem natürlichen städtischen Lebensort kämpfen. Zusammenfassend geben uns unsere Ergebnisse und das neue Verfahren einen tieferen Einblick in die Wirkungen der Verstädterung auf den Haussperlingen und diese helfen hoffentlich die Ökologie der urbanisierten Vögel besser verstehen.

KIVONAT *(magyarul)*

Az utóbbi évtizedekben az ember egyre gyorsuló ütemben és egyre nagyobb mértékben alakítja át a Föld arculatát – ennek részeként nagyon jelentős szerepet játszik az urbanizáció, vagyis a természetes élőhelyek városi területekké alakítása. Jelentősége ellenére az urbanizáció élőlényekre és azok populációit szabályozó ökológiai folyamatokra gyakorolt hatásai mindmáig nem ismertek kielégítően. Jelen tanulmány az urbanizáció egyedi és populációs szintű hatásait vizsgálja, modellfajául pedig a házi veréb *(Passer domesticus)* szolgál, mely madár, az emberi településekhez kötődő életmódja okán, talán a legismertebb madárfaj az egész világon. Vizsgálataink során az urbanizációs gradiens megközelítést alkalmazva, szabadon élő és fogságban lévő madarakon egyaránt végeztünk megfigyeléseket és kísérleteket, valamint több populációban is nyomon követtük a fészkelési sikert. Célunk volt, hogy (i) összehasonlítsuk a városi és kevésbé urbanizált területek felnőtt madarainak kondícióját, (ii) összevessük a szaporodási sikert és fiókafejlődést különböző urbanizáltságú élőhelyek madarai között, (iii) felmérjük a környezeti és genetikai tényezők jelentőségét a fiókafejlődési időszakban, (iv) valamint összehasonlítsuk a városi és vidéki élőhelyekről származó verebek ragadozókkal szembeni kockázatvállalásának mértékét, (v) továbbá validáljunk és bemutassunk egy olyan módszert, mellyel az élőhely-urbanizáció mértéke számszerűsíthető felszínborítási adatokból. Eredményeink szerint a városokban élő, kifejlett egyedek kisebb méretűek, ám nem mutatják fokozott stressz jeleit (azaz nincsenek rosszabb kondícióban). Kimutattuk továbbá, az urbanizáltabb élőhelyeken költő párok mind kiröptetett fiókáik számát, mind azok méreteit tekintve elmaradnak vidéki fajtársaik mögött; a tapasztalt különbségekért pedig a rosszabb minőségű fiókakori táplálék lehet felelős. További eredményeink szerint a szimulált karvalytámadások esetén erősebb viselkedési válaszokat mértünk a városi verebek esetében, mely arra enged következtetni, hogy ezek a madarak eredeti élőhelyeiken is nagyobb karvalyok jelentette predációs kockázatnak vannak kitéve. Összegezve, a jelen tanulmányban közölt eredmények és az urbanizáció számszerű mérésére bemutatott módszer együtt mélyebb betekintést engednek az urbanizáció házi verébre gyakorolt hatásaiba, így remélhetőleg segítik a városi madárpopulációk ökológiájának alaposabb megismerését is.

CHAPTER I

General introduction

1. Urbanization as a worldwide phenomenon

Our planet is urbanizing inevitably as Earth's urban-dwelling human population is swelling by one million per week nowadays. While in 1950 only 30% of the world's people lived in cities, in 2008 the urban population has exceeded the world's rural population – and this ratio is expected to reach 70% by around 2050 (UN-habitat 2010/11). This growth rate in the last decades has been particularly rapid in developing countries of Africa, Asia and Latin America (Lee 2007). With this urbanization related demographic expansion the number and extension of human settlements are also increasing rapidly, and so do the global environmental pressures waking in the heels of urbanization. In our recent life urbanization is one of the major factors shaping our planet's face by creating heterotrophic ecosystems that do not depend primarily on local natural resources to exist (Collins *et al.* 2000). Cities can be characterized by seriously altered energy flux, nutrient cycles, hydrology and heat balance, highly elevated pollution levels (e.g. Collins *et al.* 2000), and are generating several other problems in fields like global economy, demography, public health or human well-being (UN-habitat 2010/11). Urbanized areas are also examples of extreme anthropogenic landscape transformations. The changes in land-use, the great proportion of artificial and impermeable surface coverings (e.g. buildings, paved areas), the altered and maintained vegetation, the introduction of exotic species, the high human population densities and vast amounts of garbage have deep impacts on biodiversity and ecosystems (Pickett *et al.* 2011). Thus, urban landscapes represent unique ecosystems differing distinctly from natural or rural ones in several features.

2. Urbanization: effects on various components of the environment

Human activities related to urbanization substantially alter a diverse array of environmental components such as meteorological factors (e.g. air pollution, temperature, wind) that influence urban climate (Parlow 2011) and urban-associated flora and fauna. The phenomenon called "urban heat island effect" is one of the best documented climatic feature of cities, referring to the higher temperatures of urban areas compared to their surroundings (Collins *et al.* 2000; Kalnay & Cei 2003). The difference between urban and non-urban temperatures can be several degrees on average, especially noticeable after sunset when the absorbed heat during daytime is reemitted (Pickett *et al.* 2011). Animal and plant populations may respond to the elevated temperature in several ways, e.g. reflected in their phenology (Chace & Walsh 2006; Neil & Wu 2006; Raupp *et al.* 2010) which have important implications in population dynamics and animal-plant interactions.

Cities are also sources of many types of pollution, with concentrations several times higher than the global average. Air, soil and water pollution (e.g. gas emissions from industry, traffic and heating, or nutrient loads to water bodies) cause changes in biogeochemical and nutrient cycles and primary production (e.g. Grimm *et al.* 2008); although the pollutants' exact mode of action are still not well understood (Pickett *et al.* 2011). Their effects may expand even well beyond city boundaries and can be detrimental for many organisms, as in the case of some flowering plants (e.g. Neil & Wu 2006), terrestrial arthropods from decomposer and predator guilds (Zvereva & Kozlov 2010), amphibians (e.g. Snodgrass *et al.* 2008) or birds (e.g. Eeva *et al.* 1998, 2003), especially when they are at higher trophic levels, bioaccumulating greater amounts of heavy metals in their tissues. However, the effects of pollutants may even be beneficial to organisms both at individual and at population levels, as it was suggested by e.g. the enhanced growth of some plants (Gregg *et al.* 2003) or the increased populations of certain herbivore arthropods, the latter being probably due to the changes in their hosts' quality (Raupp *et al.* 2010).

Ecological light pollution is another characteristic disturbance related to urban settlements, altering natural light regimes in terrestrial and aquatic ecosystems. It has complex and subtle effects mainly on animal behaviour via affecting animals' orientation, migration, foraging, reproduction and communication (reviewed by Longcore & Rich 2004), and may result in forming new interactions of resource competition (e.g. Petren & Case 1996) or predator-prey relationships (Perry & Fisher 2006) between species that would not meet normally. Artificial nightlighting has demonstrable effects on a wide range of animal taxa including flying insects (Eisenbeis & Hänel 2009), diurnal and nocturnal amphibians and reptiles (Buchanan 2006; Salmon 2006; Perry *et al.* 2008), nocturnal mammals (Beier 2006; Boldogh *et al.* 2007) and birds (Gauthreaux & Belser 2006).

Anthropogenic noise pollution refers to the altered acoustic environment of cities and transportation networks. It has impacts on animal communication systems and behaviour by masking acoustic signals related to territorial defence, mate attraction, alarm calls, pair-bond maintaining calls etc. (Warren *et al.* 2006). For example, a recent study (Schroeder *et al.* 2012) on house sparrows has found that parents breeding in chronic noise reach lower reproductive success compared to parents of control areas – supposedly because elevated noise masks parent-offspring vocal communication. Noise pollution may also affect other aspects of behavior, e.g. it may interfere with sounds playing important roles in predator-prey interactions (Barber *et al.* 2009). For example, in elevated background noise chaffinches (*Fringilla coelebs*) are demonstrated to increase their vigilance and reduce their pecking rate during foraging (Quinn *et al.* 2006), and in tree swallows (*Tachycineta bicolor*) experimentally elevated static noise reduced nestlings' ability to respond parental alarm calls properly (McIntyre 2013). The potential effects of anthropogenic noise are studied mainly on bats on anuran chorus behaviour and urban birds' songs (e.g. reviewed by Barber *et al.* 2009); since anthropogenic noise is concentrated mainly at low frequencies (Warren *et al.* 2006), bird species using high-frequency songs (masked less by urban noise) supposed to be in selective advantage compared to species with lower-frequency songs – this may result in the success or failure of certain species in urban environments. In European robins *(Erithacus rubecula)* it has been experimentally demonstrated that noise level affects both spatial distribution of males (they are avoiding noise emitting sources) and their singing behaviour (McLaughlin & Kunc 2013). However, it seems that both some bird species (Slabbeekorn & Peet 2003; Brumm 2004; Slabbeekorn & den Boer-Visser 2006; Wood & Yezerinac 2006) and anuran species (Parris *et al.* 2009) can be able to compensate for elevated noise level by altering their signal characteristics due to either behavioural plasticity or evolutionary adaptation. Interestingly, noise pollution may also offer an explanation to the phenomenon of nocturnal singing of diurnal birds in cities: it could be an adaptive behavioural response by which birds try to avoid daytime acoustic interference while singing (Fuller *et al.* 2007).

Roads are prominent features of urbanized landscapes, influencing directly and indirectly the flora and fauna, and ecological processes well beyond their physical boundaries (Forman 2003). Roads are sources of various types of pollutants via related traffic, they alter a number of abiotic environmental components and modify hydrological systems (Coffin 2007). Besides these, they pose additional threats to wildlife, including habitat loss and fragmentation ('barrier effect'), direct mortality by collisions (Andrews *et al.* 2008) and they are also sources of increased stress, altering behaviour of animals (Benítez-Lopez *et al.* 2010). Roads serve as blockades or filters to wildlife movement, and the combined effects of increased mortality and the barrier for movement may result in a considerable impact on local populations – it decreases the rate of genetic exchange between breeding populations, lowering their viability (van der Dee 2008). The population fragmenting role of infrastructure has been described in a wide array of animal taxa (Coffin 2007) and connectivity among habitat patches in cities is known to be low in general, however, this varies from species to species. Roads are also altering species composition as they serve as conduits for dispersion and expansion of certain plant and animal species, often non-indigenous in local communities (e.g. Forman & Alexander; 1998; Coffin 2007).

Perhaps the most characteristic components of urbanized landscapes are buildings, affecting the urban flora and fauna expansively. Building covered patches are associated with increased human activity, pets, pollution, noise and light disturbance and reduced vegetation, thus, might be avoided by species susceptible to disturbance while more tolerant species may gain benefits from them (Miller *et al.* 2001). For example, certain bird or bat species preferentially roost or breed in houses and the proximity of buildings may serve as a thermal shelter for overwintering individuals (e.g. in arthropods; reviewed by Raupp *et al.* 2010). Human made structures are also sources of polarized light pollution (i.e. their artificial surfaces reflect incoming light, altering its direction of polarization). Since a diverse array of animal groups relies on polarized light for navigation (e.g. insects, ambhibians or birds), such artificial surfaces may act as ecological traps, affecting them in habitat selection, orientation or predation-prey interactions (Horváth *et al.* 2009). As of the latter, certain urban-breeding bird species (including the house sparrow *Passer domesticus*) can utilize these buildings as feeders and forage on insects caught by polarized light pollution (Robertson *et al.* 2010). Collision mortality in birds is also highly increased by the presence of buildings. Long distant migrants during their annual spring and fall routes are especially vulnerable to such risks; however, a recent study on North-American birds failed to find positive correlation between collision mortality and long-term population trends (Arnold & Zink 2011). Last but not least, with increasing building density the surface covered by vegetation is generally reduced and spatially more heterogeneous, adversely affecting the distribution, abundance and species richness of many native animal taxa. Reduced vegetation is also one of the major factors responsible for urban heat islands (see above), as vegetation cover decreases the amount of absorbed solar radiation, and cools air temperature by evapotranspiration (Pickett *et al.* 2011). Besides composition the phenology of urban vegetation has also changed: many studies demonstrated earlier blooming dates and prolonged growth period in urban compared to wildland areas, in which phenomena the reduced risk of springtime frost in cities suggested to play a remarkable role (e.g. reviewed by Neil & Wu 2006). Different flowering time may lead to reproductive isolation between urban and adjacent plant populations (i.e. decreased synchrony of pollination), and the earlier peak of phytophagous arthropod numbers may also reduce the overlapping timeframe with nestling rearing periods of long distant migrant, insectivorous bird species (Peñuelas & Filella 2001; Both et al. 2006).

The above section is far from a complete list of all the altered components affecting wildlife environment in urban areas, though it demonstrates the complex, wide range and mostly negative effects of urbanization on organisms living in man-made habitats. However, while some of these abiotic factors seem to be unique characteristics of cities (e.g. heat islands, various pollution types, severe disturbances) they can also be found far from human dominated habitats. Hence, urban environment is not unequalled because of its novel types of disturbances, but the combination, intensity and extent of these environmental features (Faeth *et al.* 2011).

3. Effects of urbanization on biodiversity and species composition

Human activities extensively alter the species richness (i.e. number of species) of animal and plant communities. Many of urbanization's aspects mentioned in the former section (e.g. pollutions, great amount of paved surfaces, fragmentation) have detrimental impacts on several species, hence decrease species diversity in urban areas. However, not all the effects of urbanization are necessarily negative to urban ecosystems. By transforming landscapes, human activity creates new types of habitats with altered environmental characteristics that never existed before. Studies on plants show that overall species richness increases in urban areas, probably resulting from the heterogeneous habitat patches, and introduction and maintenance of exotic ornamental species (Zipperer *et al.* 1997; Grimm *et al.* 2008). In animals, the most studied groups (arthropods, birds and mammals) exhibit lower species richness in general, with the lowest diversities documented in urban core areas (reviewed by McKinney 2002, 2008). However, decrease in species richness with increasing urbanization is not strictly monotonic, as avian species richness often tends to peak at intermediate levels of urbanization (e.g. Marlzuff 2001, 2005; Chace & Walsh 2006), but such pattern is also known for butterflies (Blair & Launer, 1997; Blair 1999; or reviewed by Raupp *et al.* 2010). Less studied taxa (e.g. amphibians) also show decreased species richness, simplified community structure and lower genetic variability with increasing urbanization (Hamer & McDonnell 2008).

Besides biodiversity, urbanization also influences species composition of the avifauna. According to the terminology of Blair (1996), bird species of urban areas can be categorized as 'urban avoiders', 'urban adapters' and 'urban exploiters', differing e.g. in the degree to which they can utilize and rely on human-provided resources (McKinney 2002). Typical *urban avoiders* are species that are very sensitive to human-related disturbances (e.g. large raptors), or are habitat specialists, e.g. nesting on the ground or feeding on arthropods. These species are mostly native in a community and can be found in relatively undisturbed habitats (consisting mainly of native vegetation) outside of cities. Urban avoiders are the most adversely affected by urbanization, resulting in their abundance to be the lowest in urban areas. The next subset of birds, the *urban adapters* are often 'edge species', residing in areas with intermediate levels of disturbance (e.g. suburbs), and besides natural resources they facultatively utilize a remarkable proportion of human provided resources, e.g. food from garbage or bird feeders. Cavity or shrub nesters, and omnivore and ground feeding species are typical in this category, such as members of families *Corvidae* or *Paridae* (e.g. Croci *et al.* 2008), or many ground feeding finch species. Urban adapters include both native and non-native species, and they tend to be dominant in the rural to urban transition areas (intermediate development), where land-use is most heterogeneous. The abundance peak of the third group, the *urban exploiters* (or synanthropic species, referring to that they are cohabiting with humans; Johnston 2001) can be found in the most urbanized areas, where native habitats are scarce and human-altered conditions are predominant. These communities are characterized by a few prevailing and often alien species, and by very few of local native ones; furthermore, their diversity and abundance is usually not dependent upon vegetation (e.g. reviewed by McKinney 2006). These species not only exploit but often have become dependent on sources provided by humans (Shochat *et al.* 2006); the feral pigeon *(Columba livia)*, house sparrow, European starling *(Sturnus vulgaris)*, house crow *(Corvus splendens)*, common myna *(Acridotheres tristis)* in Australia or India, the house finch *(Haemorhous mexicanus)* in North America, or birds of prey like the peregrine falcon *(Falco peregrinus)* are common examples in this category. Compared to urban adapters, which are often early successional species from more natural habitats adjacent to cities, exploiters are well adapted to human-dominated landscapes, often sharing a long common history with humans (e.g. the house sparrow, Ericson 1997; Saetre *et al.* 2012).

Further general aspects of species composition are that the proportion of exotic species increases toward heavily urbanized areas (Marlzuff 2001; McKinney 2006; Lepczyk *et al.* 2008; van Rensburg *et al.* 2009) and that urban bird communities are structurally simpler compared to those of more natural areas. This pattern is the consequence of human activities related to cities, in terms of both introducing non-native individuals (willingly or accidentally), and by creating habitats that are similar to each other (especially in urban cores) even if they are in different regions of Earth (McKinney 2006; Sorace & Gustin 2008). Accordingly, in Britain, Evans *et al.* (2009d) did not find latitudinal gradient in avian species richness in cities, despite the fact that such gradients have been shown in non-urban areas of Europe. These altered habitats support only a low number of generalist species that are often the same in many cities. These species are proposed to be (pre)adapted to human-created conditions, thus are able to flourish in urban areas all over the world, while competitively exclude non-synanthropic species (Shochat *et al.* 2010). This phenomenon has been referred to as ‘biotic homogenization’ (McKinney 2006), including both taxonomic (reduced number of species) and functional homogenization (dominance of generalist over specialist species). Not surprisingly, the retention of native vegetation enhances the response of native faunal elements and also, increasing vegetation cover also increases species richness in the urban matrix (reviewed by Luck & Smallbone 2010).

4. Mechanisms generating changes in urban avian communities

Besides the reduced biodiversity, an other characteristic pattern of urban bird communities is the often dramatic increase in overall population densities compared to adjacent, natural ecosystems; although, usually only a few species contribute the majority of individuals (e.g. Marlzuff 2001; Chace & Walsh 2006). Human-related factors affecting the urban avifauna have been partially covered above (*section 2*), including many negative, mostly indirect effects. However, there are a few positive effects of human activities to birds, e.g. the availability of extra nest sites (nest boxes, roofs, crevices) and the increased food abundance – the latter of which is probably the most important one of them. According to this, the remarkable difference between urban and rural avian population densities is suggested to be driven by human-influenced food webs, i.e. by the highly increased and predictable food resources and the low predation risk associated with urban areas (Shochat 2004; Shochat *et al.* 2006; Anderies *et al.* 2007). I will discuss both of these assumptions in detail below.

The changes in resource-based forces (‘bottom-up effect’) either as the increased primary productivity from human activities or the human provided food sources (e.g. seed in bird feeders and communal waste) are profound interventions to urban food supply dynamics. Since these supplementary food sources reduce the risk of starvation and may enhance reproduction (Robb *et al.* 2008), the increase in abundance and predictability of food is often accepted as a major driver of the extremely increased avian biomass of urban areas (Fuller *et al.* 2008). However, this bottom-up effect is paradoxical, since despite the abundant resources (at population level) the high density of consumers may reduce the per capita amount of food (at individual level) due to the supposedly strong competition. This could result in a resource overmatching where, ultimately, most urban individuals may not reach higher fitness compared to individuals of nonurban areas. A competition model (‘credit card hypothesis’; Shochat 2004) has been suggested to resolve this paradox by emphasizing the role of continuous and predictable food input in cities. The theory suggests that, on the one hand, the increased avian biomass in urban areas consists mainly of poor quality individuals with inferior competitive abilities and low body reserves that can live only on a day-to-day basis in cities but would be removed by natural selection in environments with more unpredictable resource renewal. They are the losers of the competition, ‘living on the credit of tomorrow’. Such individuals’ contribution to next generation is small, however they are accounting for a significant proportion of urban populations. On the other hand, the case of competition’s winners is just the contrary: they constitute the minority of the urban population, while only they are able to maintain high body reserves enough to successfully reproduce. Furthermore, food predictability is hypothesized to alter the reproduction investment of these winners, as they may invest in producing more offspring with lower body condition as a response to the increased chance of post-fledging survival. Additionally, it is also important to note that though the overall food quantity may be elevated in cities, the altered palette of available food sources contains high proportion of anthropogenic food – which can be appropriate for adult individuals, but not so for nestlings, further contributing to fledglings' reduced body condition (e.g. in European starlings, Mennechez & Clergeau 2001, 2006; or Western gulls (*Larus occidentalis*) Pierotti & Annett 2001). Therefore, according to the theory's assumptions, we should find larger populations with individuals of generally inferior body condition and competitive performance, and lower average fitness in urban areas, and also higher variance in these traits.

The consumer-based forces of urban food webs are also substantially influenced by human activities. The changes in 'top-down control' are rather complex and their importance as a driver of urban bird community dynamics is poorly understood. The term 'top-down effect' refers to the common assumption of reduced predation pressure in urban areas (also known as 'safe zone hypothesis') which is mainly based on urban birds' reduced fearfulness to humans and the low abundance of their native predators (Gering & Blair 1999; Shochat *et al.* 2006). This predation relaxation is suggested to partially explain the great biomass of avian prey species in cities. On one hand, there are studies reporting higher or similar survival rates of prey species in urban areas (e.g. reviewed by Evans 2010; Fischer *et al.* 2012) which may be due to lower predation rates compared to rural habitats. This is an indirect approach, however, as higher survival rates may result from several other factors (e.g. more predictable food, milder climate or decreased mortality as a consequence of reduced migratoriness). On the other hand, contrarily to the predation relaxation assumption, the overall abundances of certain potential predators, like corvids (Jokimäki & Huhta 2000; Marlzuff *et al.* 2001b; Marlzuff & Neatherlin 2006) or mammalian, omnivorous mesopredators (e.g. raccoons, mustelids; Prange *et al.* 2003; Herr *et al.* 2008; Tóth *et al.* 2011) are frequently higher in urban environments compared to adjacent, more natural habitats (Rodewald *et al.* 2011). Likewise, non-native mesopredator species, e.g. the domestic cat (*Felis catus*) can reach extremely high densities in cities, exceeding the numbers of any of the native predator species, far above natural carrying capacity (Lepczyk *et al.* 2003; Baker *et al.* 2008; Sims *et al.* 2008). The fact that these predators reach the highest numbers in urban habitats (e.g. Haskell *et al.* 2001; Sorace 2002), yet their avian prey species also thrive there in great numbers, entail contradictory predictions on the importance of 'top-down control', leading to a 'predation paradox' which seems to be a widespread phenomenon in urban habitats (Fischer *et al.* 2012). However, different types of predation cannot be treated as one; it is important to draw distinction between predation in egg/nestling and adult stages of prey species as both the involved predator species and the predation risk may be different. This paradox questions if urban bird populations are strongly top-down regulated (Shochat 2004) and it is challenging to resolve this contradiction, because a number of reasons make it difficult to assess the actual impact of urban predators to the avifauna.

First, response of predators to human environmental alteration is complex. Like in the case of prey species, urbanization filters different predator species as well, favoring generalists over specialists along the urbanization gradient (e.g. Jokimäki & Huhta 2000; Sorace & Gustin 2008). Besides, the absence of vulnerable apex-predator species may lead to 'mesopredator release' (Ritchie & Johnson 2009) in urbanized areas, indirectly increasing predation rates of both nests and fledged birds (Rogers & Caro 1998; Crooks & Soulé 1999). Response of raptor species to urbanization is also highly species-specific: some carnivorous bird species that were formerly absent as breeders in urban areas, have been documented to establish breeding populations within cities recently, like the Eurasian sparrowhawk (*Accipiter nisus*), the northern goshawk (*Accipiter gentilis*) or the Eurasian kestrel (*Falco tinnunculus*), supposedly following their abundant prey populations into cities (e.g. Kübler *et al.* 2005; Chace & Walsh 2006; Rutz 2008). As a general pattern it seems that large bodied carnivores and snake species respond negatively to urbanization, while generalist bird and omnivorous mammal predators fare much better in urban environments reaching high abundances, especially in the case of some introduced predators. Thus, as a conclusion it is possible that the total density of vertebrate predators in urbanized habitats is similar to or exceeds that of exurban areas (Fischer *et al.* 2012).

Second, despite the high densities of urban predators it is debated that whether these potential predators act as actual predators or rather rely more or less on anthropogenic, easily accessible food sources (e.g. garbage or food subsidized for pets). If omnivorous predators shift their diet and consume alternative food sources instead of hunting, it can result in lower actual predation rates on prey species than it would be assumed simply by predators' abundance alone (e.g. Rodewald *et al.* 2011).

Third, predation on fledged birds (juveniles and adults) and predation on nests are two different scenarios, involving different species as main predators. These two groups of predators may have different abundances in cities, thereby having different impact on avian communities. Raptor species prevailingly prey upon adult birds; domestic cats also pose threat mainly to fledged birds (especially to juveniles), however, their role as nest predators in urban areas is also documented (Rodewald & Kearns 2011; Stracey 2011). Given their densities it is not surprising that cat predation is considered among the most important human-related causes of bird mortality (Baker *et al.* 2005; Dauphiné *et al.* 2009). At the same time many feral, mammalian mesopredators and corvids (magpies, jays and crows) are usually known to prey upon eggs and nestlings (e.g. Jokimäki & Huhta 2000; Marlzuff *et al.* 2001b) and are reported to depredate more nests in urbanized compared to rural habitats (Rodewald & Kearns 2011), also reflecting relationships between predator community composition and level of urbanization.

A major implication of all these points is that estimation of predation pressure based solely on predator density in urban areas is not satisfying, since high predator abundance does not necessarily indicate high actual predation pressure. Predators' effects on prey populations are complex and manifold, as predation risk may change behavior of prey, even via indirect effects, being detrimental to prey species (Cresswell 2008); predators can decrease prey population size by killing; and natural selection due to modified predation pressure may lead to morphological or behavioral adaptations of prey in cities. Thus, different approaches are needed to get a more precise picture on how predation pressure changes along the urbanization gradient.

5. Adaptations to urbanization

As urbanization poses a significant threat to biodiversity it is important to identify the biological traits of successfully urbanized bird species that help them tolerate or adapt to urban environments. According to the results of a global interspecific comparative study (Bonier *et al.* 2007), urbanization tends to favour, in general, species that possess broader environmental tolerance (indicated by their broader elevational and latitudinal breeding ranges), i.e. being generalists. Further studies suggest that successful urban species are characterized by omnivorous or granivorous diet, nesting on open rock surfaces (i.e. on buildings) or in cavities, in addition living in social groups and being non-migratory (Chace & Walsh 2006; Kark *et al.* 2007). High annual fecundity (i.e. short generation times and multiple broods per year) is also suggested to enhance successful urbanization of species (e.g. Møller 2009), as it may promote both the relative fast appearance of genetic adaptations to novel environments and also population recovery from disturbance. Beyond these there are other traits of successful urban invaders, like high dispersal ability, reduced fear of humans, large relative brain size, high levels of innovative ability and behavioural flexibility (e.g. Sol *et al.* 2002; Møller 2009). It seems, thus, that no single trait can indicate a bird species' success in urbanized habitats, but a combination of them (Croci *et al.* 2008). However, a recent study (Evans *et al.* 2011) that applied the ratio of urban to rural population densities of bird species instead of other, formerly used indices (e.g. binary classification [i.e. a species is present / breeding in urban areas, or not] or urban population densities alone) has found results contrary to those of former studies. Evans *et al.* reported limited evidence for links between urbanization and traits such as breeding range size, long-distance migration, dispersal ability, high annual fecundity, relative brain size and invertebrate adult diet. However, similarly to former works (e.g. Chace & Walsh 2006), they reported lower urbanization in ground-nesting species, and a tendency for higher urban densities of species that have plant material in their adult diet, supposedly because of taking advantage of supplementary feeding. Their results also supported that in cities generalist species are favoured over specialist ones, albeit this was dependent of the exact manner of defining 'ecological specialization'. An other, supposedly important trait of successful urban-dweller birds is their reduced fearfulness to humans. A recent study (Carrete & Tella 2011) conducted in newly urbanized areas of South America, has found that urban invader species are characterized by large relative brain size (a surrogate often applied to measure behavioural flexibility), and high inter-individual variability in fearfulness. Large relative brain size can be important as behavioural flexibility may yield fitness benefits to individuals in altered or novel environments (Sol *et al.* 2005), while the latter finding fits into the theory that in species exhibiting high variability in fear response in their natural habitats, urban invader individuals may be the subset of bolder individuals (Møller 2010). Increased boldness toward anthropogenic disturbances is hypothesized to be beneficial in urban areas, thus evolved as an adaptation (Møller 2008), when most of the passing humans do not pose threat to an individual. Additionally, increased boldness may also affect other aspects of behaviour. For example, in song sparrows (*Melospiza melodia*) both increased boldness to humans and increased territorial aggression was found in urban compared to rural populations (J. Evans *et al*. 2010), the increased aggressiveness may possibly driven by the higher population densities in cities.

The European blackbird *(Turdus merula)* is a good example of a successfully urbanized bird species. Since the early 19th century it has expanded its range into many cities both within its native range (Western Palearctic) and in different parts of the world (Sol *et al.* 2002), possibly as a result of several independent colonization events (Evans *et al.* 2009a). Since selection pressures differ between urban and adjacent natural habitats, it is plausible to expect trait divergence between a species' rural and urban populations. Populations of the European blackbird provide examples of such urbanization related trait divergence: the species' urban individuals are less fearful of humans, breed and moult earlier, are less migratory, have longer period of daily activity (Partecke *et al.* 2006a) and show lower stress responses compared to forest-living individuals (Partecke *et al.* 2006b). However, it is a question whether these 'urbanized traits' result from genetic adaptation or from mainly phenotypic plasticity (which softens the force of natural selection on genetic variation). Results of common-garden experiments on the species suggest that genetic differences are responsible for changes in urban individuals' stress physiology (Partecke *et al.* 2006b), urban males' reduced migratoriness and earlier annual gonad development (Partecke & Gwinner 2007). Lower acute stress response is supposed to be beneficial for urbanized birds since with such down-regulation mechanisms they can tolerate more frequent anthropogenic disturbances. As of a consequence, their populations may be able to flourish in cities where other species (without such modification of stress response) may not so. Since in cities the chance of overwinter survival is increased due to milder climate (see 'urban heat island' effect) and continuous food supply, reduced migratory may be profitable for an individual as it can occupy territory earlier and start breeding before migratory competitors arrive. Albeit the above, divergent traits are likely involve genetic changes, a study targeted at randomly selected neutral loci has not demonstrated genetic divergence between individuals of urban and adjacent non-urban areas, although it involved only one forest and one urban population (Partecke *et al.* 2006a). Recently, however, a larger-scale study (Mueller *et al.* 2013) conducted in 12 urban and rural population pairs of blackbirds compared several candidate genes expected to be important in urbanization. One of the candidate loci (SERT gene, supposedly playing role in harm avoidance behaviour) has been found to show genetic divergence in the great majority of the studied paired populations. As this gene is linked to anxiety-related traits, it has been suggested that the adaptive value of such behaviours may be different between rural and highly disturbed urban environments, in this manner it may be a target of directional selection. Such rapid evolution and trait divergence is also documented in the case of dark-eyed juncos *(Junco hyemalis)* where a small population of individuals has colonized and became established in an urban environment. During the roughly two decades of urban life the population has lost approximately 22% of white coloration in tail feathers compared to the members of the original, mountain-dwelling population; the change has been attributed to the result of relaxed sexual selection in the urban environment (Yeh 2004).

Many species' urban populations are genetically divergent from rural ones (i.e. intraspecific variation) and exhibit reduced genetic diversity, although the variation in the magnitude of both genetic differentiation and reduction is widely different between species and locations (Evans 2010). Such divergence may arise, in part, from new genetic adaptations to altered selection pressures in cities (e.g. as in the blackbird, see above) or may be the result of urban populations' reduced genetic diversity which seems to be typical compared to nonurban populations (Evans 2010). According to this, observed trait divergences between urban and rural populations may be unrelated to habitat-specific adaptations, instead being the outcome of founder effect (due to a colonizing population's bottleneck), or limited dispersal capacity (Evans *et al.* 2009a; Evans 2010). The house sparrow could give an example to the latter, as in Belgium, Vangestel reported small-scale genetic population structure in urban and rural house sparrows, higher levels of average relatedness in urban individuals (suggested to be the result of more limited dispersal in urban populations; Vangestel *et al.* 2011b) and smaller home ranges in the city (Vangestel *et al.* 2010). In rural England, Hole *et al.* (2002) reported significant genetic differences between locally isolated rural sparrow populations, and similarly to this, urban individuals of the European blackbird tend to be more sedentary (Partecke & Gwinner 2007), which may further promote urban populations' genetic divergence. However, genetic divergence of populations is highly affected by local topological heterogeneity and geographical connectivity between local populations. For example, a study on Finnish house sparrow populations concluded that in the 1980s the whole country's population was panmictic and genetically very homogenous (Kekkonen *et al.* 2011), in contrast with island populations in Norway (Jensen *et al.* 2013) where even relatively close populations showed genetic divergence in microsatellite loci and signatures of population bottlenecks, suggested to be due to the more heterogeneous landscape.

However, the European blackbird is a rare example of a species in which several traits have been studied in response to urbanization. Our knowledge on trait divergence and its fitness consequences, the rate of differentiation between rural and urban populations and the drivers is still very scanty for drawing generalized conclusions about how birds adapt to urban environments (Evans 2010).

6. General introduction of the human commensalism and recent status of house sparrow

The house sparrow belongs to the sparrow family *(Passeridae)*, order passerines *(Passeriformes)*, and is one of the most familiar and abundant land bird species across the world. The species is a very successful human commensalist, and unique in the term of its dependence on human presence. It has taken advantage of human-altered habitats, and currently it can be found across the urban-rural gradient, from remote farmlands to metropolitan core regions. Outside its original breeding range (Asia, Europe and Northern Africa), the house sparrow has been introduced to all of the continents (except Antarctica) and to many oceanic islands, where it has spread successfully (Anderson 2006).

It is clear that the species has a long commensal relationship with sedentary humans. The house sparrow is assumed to have evolved as a species in the Middle East, approximately 400.000 years ago, and proposed to have spread across its native range and form its commensal relationship with humans with agriculture somewhat 10.000 years ago (Johnston & Klitz 1977). However, its earliest fossil evidences suggest a much earlier relationship with humans, long before the advent of agriculture (Anderson 2006). As of alternatives of its origin, studies based on enzyme polymorphism (Parkin 1988) and mitochondrial DNA (Allende *et al.* 2001) date its speciation either to a much more recent or earlier date, respectively. Concerning the origin of its commensalism, two main hypotheses have arisen. One of them suggests an early split of the ancestral sparrows resulting two major lines (the Palearctic *domesticus* and the Oriental *indicus* groups), implying that synanthropism evolved in the two regions after the split, independently. The other hypothesis suggests expansion from a single source, followed by a recent morphological differentiation between the two groups, thus assuming that commensalism has arisen only once in the ancient population (Anderson 2006). A recent study, based on the genetic analysis of mitochondrial DNA found no evidence of any early split between the two subgroups, thus supports the theory of single origin of commensalism and a rapid divergence in recent plumage traits (Saetre *et al.* 2012). The authors also suggest that the species' expansion occurred 3500-7000 years ago, following the rise and spread of agriculture and human settlements, and that ancient sparrows' ecology might have been similar to that of the subspecies *P. d. bactrianus*, which is the sole exception in the group with being migratory and breeding preferentially in natural grassland habitats. All in all, the house sparrow is suggested to have arisen as an obligate human commensal because of the year-round access to stored grain in human settlements and since then it shares a very long, common history with humans (Anderson 2006).

Despite its worldwide success in human-made habitats, in the last few decades populations of the house sparrow have undergone remarkable declines in many areas of its range. This trend gained much attention (e.g. Summers-Smith 2003; De Laet & Summers-Smith 2007), especially in Britain where the species' population dynamics is the best documented (e.g. Robinson *et al.* 2005). However, this pattern is complicated, as there are areas without signs of decline (e.g. Scotland and Wales; Siriwardena *et al.* 2002), including some European cities (e.g. Manchester or Berlin; De Laet & Summers-Smith 2007), and also because in populations that suffered major loss, the timing and the magnitude of decline are different in urban and rural areas (Crick *et al.* 2002). This fact and the supposedly little interchange between rural and urban populations suggest that different mechanisms are driving the changes in rural and urban habitats. While the Britain farmland population declined to 60% and seems to have stabilized at that level in the 1980's, it appears that population declines have been far more prominent in urban regions (Summers-Smith 2005), at least in North-Western Europe (for an overview of population trends in European big cities see Shaw *et al.* 2008). However, the view that different causes are responsible for the urbanization-dependent decline is not unequivocal and has been questioned by some studies (Bell *et al.* 2010; Bell 2011).

A number of causal factors have been proposed to be responsible for the decline in urban areas (e.g. see the reports of Summers-Smith 2003 or Crick *et al.* 2002), Factors behind the species' decline may include increased predation by free-ranging pets and urbanized raptors (e.g. Baker *et al.* 2008; Bell *et al.* 2010); changes in human socioeconomic status (i.e. lower proportion of unbuilt, brown field areas, and higher proportion of exotic plants, loss of suitable nesting sites in modernized buildings; Shaw *et al.* 2008); diseases; shortage of invertebrate nestling food (e.g. Peach *et al.* 2008) or environmental pollution (e.g. Summers-Smith 2003). As the general trends of the species' decline are not consistent, it can be assumed that a combination of the above factors is responsible for the dramatic decline of urban sparrows. I will discuss the possible causes of decline in detail in ***Chapters IV*** and ***VII.***

Liker and colleagues (2008) investigated the relationship between habitat urbanization and morphological characteristics of house sparrows in Hungary. They measured more than 1000 adult individuals from 7 different sites along the urbanization gradient, and found that birds' body mass and tarsus length (i.e. body size) differed significantly in respect to urbanization, with individuals in more urbanized habitats being lighter and smaller than their rural conspecifics. Similarly to this, reduced body size in urban areas was found in a variety of other vertebrate and invertebrate taxa (Evans 2010).

A further interesting finding of the Liker *et al.* (2008) study was that the difference in body mass between urban and rural sparrows persisted even when they were kept for months in aviaries among identical conditions, with unconstrained food supply. The authors concluded that reduced body mass was not the detrimental effect of limited food access of urban adults, since urban sparrows have not compensated for their lower body mass during the captivity. Instead, the authors suggested that lower body size and mass might be (a) an adaptive response of urban populations to higher predation pressure and / or to milder microclimate in cities (directional selection), or (b) due to habitat differences in nestling development (i.e. inadequate quality and/or quantity of nestling food). However, based on their results it cannot be excluded that lower body mass and size was an indicator of urban individuals' inferior quality, being a consequence of elevated levels of stressors (e.g. pollutions, lower food quality, or stronger competition) in cities, as predicted by Shochat's (2004) theory.

CHAPTER II

Thesis objectives

In this thesis my general aim was to better understand the effects of urbanization on birds, both at individual and at population levels. In the following studies I used the house sparrow as a model species, and investigated individual body condition, breeding performance, nestling development and perceived predation risk along the urban-rural gradient. Additionally, since quantifying the urban-rural gradient is essential for studying animals' response to habitat urbanization, I also introduced a newly developed, semi-automated method to quantitatively estimate the intensity of habitat urbanization from satellite images. Finally, my further intent was to contribute to the understanding of the reasons lying behind the puzzling, general decline of house sparrow in many parts of its range, particularly in urban areas. The studies below were carried out in collaboration with the Ornithological Research Group at the University of Pannonia. I participated in all phases of the work detailed in the following chapters, from planning of the studies to the writing of the manuscripts.

1. Individual quality and body condition of adult house sparrows in differently urbanized habitats

In ***Chapter III*** we investigated the relationship between adult birds' body condition and the degree of their habitats' urbanization. The starting point of this study was that Liker and colleagues (2008) had found urban sparrows to be smaller compared to rural ones (as described above). This smaller body size could be the result of inferior individual quality, thus may indicate suboptimal environmental conditions in urban habitats. Urbanization exposes organisms to a wide range of altered environmental factors, many of these are proposed to be stressors (see the *General introduction* in ***Chapter I***). Furthermore, the large amounts of highly predictable (but often lower quality) food sources and the higher densities of urban exploiter species predict strong competition for food, resulting in low per capita amount of food and, finally, in individuals with inferior body condition – as it was suggested by some studies (e.g. Shochat 2004; Shochat *et al.* 2006; Anderies 2007). To investigate whether the smaller body size and mass indicates inferior body condition, we used several indices of morphological, hematological, hormonal and plumage traits of birds from differently urbanized habitats to assess and compare their individual body condition.

2. Differences in reproductive success and nestling development of free-living urban and rural house sparrows

In the first part of ***Chapter IV*** our aim was to study and present population trends of the species in Hungary between 1999 and 2011 and, furthermore, to compare the reproductive success and nestling development of sparrows between differently urbanized habitats. We were also curious whether the formerly identified smaller size of urban adult sparrows appears at individuals' early developmental stage, and if it does, can it be explained by any differences in parents' provisioning efforts and/or differences in nestling's diet. To answer these questions we monitored sparrows' breeding performance in several habitats throughout two consecutive years, and also collected observations on parents' feeding behavior from three years by video recording parental provisioning at rural and suburban nests.

3. Assessing the importance of genetic factors vs. environmental conditions during nestling development

In the second part of ***Chapter IV*** we investigated whether the observed habitat differences in nestlings' body size and mass result mainly from genetic divergence or are determined by the environmental conditions during nestling development. To answer this we conducted two experiments, designed to test if nestlings originating from different habitats grow differently under identical conditions. First, we tested whether urban and rural breeding adults differ in reproductive success, chick feeding and nestling development in captivity in the same environment *(common-garden experiment).* Second, in a field experiment we swapped few days-old hatchlings between urban and rural nests and monitored their development *(cross-fostering experiment)*.

4. Differences in perceived predation risk of urban and rural house sparrows

In ***Chapter V*** the goal was to compare the perceived predation risk of urban and rural house sparrows. Because both lower and higher predation risk has been hypothesized in cities compared to rural areas, and it is difficult to test these differences from predator abundances, we chose to study the birds' perceived predation risk as inferred from their behavioral responses. We exposed adult sparrows from differently urbanized habitats to simulated predator attacks and measured their subsequent risk-taking behavior to gain information about the predation risk they may be exposed to in their original habitats.

5. Quantifying the degree of habitat urbanization using satellite images

The ecological gradient approach has been applied in many of the last decade's urban-ecology researches, and a crucial component of such studies is the methodology of measuring urbanization. In ***Chapter VI*** we describe a recently developed, semi-automated method to quantify the degree of habitat urbanization. Based on the manual scoring process formerly introduced by Liker and colleagues (2008), we developed a software to measure the degree of habitat urbanization and to generate an 'urbanization index', using land-cover patterns from freely available satellite images. We validated the 'urbanization indices' generated by our method by comparing it to measurements produced by both subjective human scoring and widely accepted geoinformatics measurements. Furthermore, we investigated the ecological applicability of the semi-automated 'urbanization indices' by applying them to the same dataset we used in ***Chapter III*** and comparing the results of the two analyses. We propose this method for studies conducted along urban-rural gradients, to promote their integration into a common context with common methodology.

CHAPTER III

Multiple indices of body condition reveal no negative effect of urbanization in adult house sparrows

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ABSTRACT

As urbanized areas expand and develop throughout the world, the importance of understanding their effects on wildlife increases. Living in cities may be stressful for animals but may also provide benefits at the same time, and the sum of these effects should manifest in the body condition of individuals. Studies addressing this phenomenon tend to evaluate one or few indices of body condition, each of which may be subject to various confounding effects and seasonal changes. In this study we used multiple approaches to assess the effects of urbanization on adult body condition in house sparrows, a passerine undergoing population declines in urban habitats. In line with earlier studies, we found that sparrows in more urbanized habitats have reduced body mass. However, birds had similar scaled mass index (body mass corrected for body size) along the urbanization gradient at all times of the year, contradicting the previous result on type-1 regression residuals. In the non-breeding season, urban and rural birds had similar levels of corticosterone, hematocrit, and heterophil:lymphocyte ratio. In the molting season, hematocrit indicated better condition in rural birds whereas H:L ratio showed the opposite; however, these trends were not consistent between age groups. Two condition-dependent plumage traits, male bib size and wing bar size, showed no systematic variation along the gradient of urbanization. These results suggest that the environmental conditions experienced by adult house sparrows are not more stressful in more urbanized habitats, and they also highlight the importance of considering multiple indices of body condition.

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1. INTRODUCTION

Natural habitats are being human-modified and converted into urbanized areas at an accelerating rate, and this process has powerful and complex effects on ecosystems (Marzluff *et al.* 2001, 2008). Urbanization exposes animals to potentially detrimental factors such as human disturbance, toxins, noise, and artificial lighting on the one hand, but can provide advantages like richer or more predictable sources of food and water, and milder climate on the other hand (Shochat *et al.* 2006). Responses to these effects are species-specific, depending on the life-history and ecological characteristics of each species (Croci *et al.* 2008; Møller 2009; Evans *et al.* 2011). As a result, urbanization alters the structure of native communities, which further changes the ecological conditions for species colonizing or inhabiting cities as they are facing a novel set of competitors, predators and parasites (Marzluff *et al.* 2001; Shochat *et al.* 2006; McKinney 2008). Understanding and predicting these processes requires thorough mechanistic ecological studies at the level of individuals (Shochat *et al.* 2006).

One of the most fundamental questions is how urbanization affects the body condition of animals. Individual condition is a "composite of factors including nutritional state, level of health, experience, and amount of physiological wear and tear" (Schluter & Gustafsson 1993) that can be a major determinant of fitness and may indicate environmental stress (Peig & Green 2009, 2010). Despite its crucial importance in animal ecology, body condition remains difficult to measure and there is currently no consensus about the most appropriate method for quantifying it in a non-destructive way (Peig & Green 2010). For example, vertebrates react to stressful challenges, including those attributable to urbanization, by a suite of neuroendocrine processes, central to which is the acute release of glucocorticoid hormones that govern metabolic and behavioral responses, enabling the animals to overcome those challenges (Romero 2004; Wikelski & Cooke 2006). However, prolonged or repeated exposure to stressors can be harmful by inhibiting growth, immune functions, and reproduction (Wingfield & Sapolsky 2003); such chronic stress may be diagnosed at several scales of body condition (Boonstra *et al.* 1998; Clinchy *et al.* 2004). At the hormonal scale, it may lead to increased concentrations of glucocorticoids in the blood stream due to the enlargement of adrenals (although certain chronic stressors can lead to decreased glucocorticoid levels; Rich & Romero 2005; Cyr & Romero 2007). At the hematological scale, chronic stress may cause anemia (red blood cell loss, reflected by a lower hematocrit) and alter the distribution of white blood cells (due to changes in immune function), often resulting in a higher heterophil to lymphocyte (H:L) ratio (Davis *et al.* 2008). At the morphological scale, loss of body weight may result since glucocorticoids stimulate energy mobilization and inhibit energy storage. Each of these measures has the potential to reveal individual differences in body condition, although their utility may vary greatly depending on species and the extent by which confounding sources of variation are taken into account (Ots *et al.* 1998; Romero 2004; Fair *et al.* 2007; Davis *et al.* 2008; Peig & Green 2009, 2010).

Up to now, several studies have investigated the above aspects of individual condition in relation to urbanization, ranging from lizards (French *et al.* 2008) to bears (Beckmann & Berger 2003), with most research focused on birds. Collectively, these studies do not outline a general effect of urbanization, as their results differ not only among but also within species (e.g. Ots *et al.* 1998; Hõrak *et al.* 2004; Partecke *et al.* 2005; Evans *et al.* 2009b), and these differences cannot be fully accounted for by each species' adaptability to urbanization (Fokidis *et al.* 2008, 2009). For example, in urban compared to rural populations, baseline levels of corticosterone (the main avian glucocorticoid hormone) were higher in tree sparrows (*Passer montanus*; Zhang *et al.* 2011) and male (but not in female) white-crowned sparrows (*Zonotricha leucophrys*; Bonier *et al.* 2007) but lower in Florida scrub-jays (*Aphelocoma coerulescens*; Schoech *et al.* 2007), whereas corticosterone levels in response to a standard acute stressor (i.e. stress response) were higher in the scrub-jays (Schoech *et al.* 2007) but lower in captive-reared blackbirds (Partecke *et al.* 2006b). One reason for such an inconsistency of findings may be that most studies were "snapshots" at different scales of body condition of different species in different life-history stages. Since each measure of body condition can be influenced by several extrinsic and intrinsic factors and may be sensitive to different aspects of environmental stress (Fair *et al.* 2007; Lendvai *et al.* 2007; Davis *et al.* 2008; Lendvai & Chastel 2008), using only one or few indicators of body condition might lead to incorrect or incomplete conclusions.

In this study, our aim is to draw a more detailed picture of the effects of urbanization on individual condition. Our study species is the house sparrow, one of the most intriguing cases of urbanization. Being a human commensalist, this species has accompanied man for centuries and became the most successfully urbanized bird until the mid-1980s; then its populations started to decline at many locations worldwide, especially in European cities (Shaw *et al.* 2008). Several hypotheses have been put forward to explain the decline of urban sparrows, including increased pollution by traffic and predation by domestic cats and sparrowhawks, and loss of nesting sites and food sources due to cities' socioeconomic changes (Summers-Smith 2003; Shaw *et al.* 2008). Recent studies showed that adults' body size and mass in the non-breeding season is smaller in more urbanized populations of house sparrows, suggesting inferior body condition for urban birds (Fokidis *et al.* 2008; Liker *et al.*, 2008; Bókony *et al.* 2010). Altogether, we can thus hypothesize that more urbanized habitats are more stressful to house sparrows.

To test this idea, here we examine various indices of environmental stress along the urbanization gradient in adult sparrows. Specifically, first we evaluated hormonal and hematological measurements of body condition during molt and at the end of the non-breeding season to test whether birds in more urbanized habitats have higher baseline and stress-induced levels of corticosterone, lower hematocrit (i.e. less red blood cells), and higher H:L ratio. Then we examined two morphological aspects of body condition. Firstly, we re-assessed whether the actual amount of energy reserves, expressed as body mass corrected for body size (Peig & Green 2009, 2010), decreases with increasing degree of habitat urbanization throughout the year, as found earlier by using a different analytical approach (Liker *et al.* 2008). Secondly, we investigated two condition-dependent traits of plumage coloration: the size of the black bib that is influenced by, among other factors, the body condition of males (Nakagawa *et al.* 2007) and the size of the white wing bar that is sensitive to nutritional conditions i.e. protein intake (Poston *et al.* 2005). Sparrows are expected to grow consistently smaller plumage ornaments in more urbanized habitats if the latter are more stressful, e.g. by providing inferior feeding conditions during molt than less urbanized habitats.

2. METHODS

2.1. Urbanization intensity measurement

We studied house sparrows at several sites along the urbanization gradient in Hungary, ranging from small, isolated farms through villages and suburbs to the most heavily built-up city centers (Table III.1). We sampled the gradient of urbanization not as a geographical gradient around a single city but as a variety of differently urbanized sites at several geographic locations (McDonnell & Hahs 2008). Urbanization of these sites was quantified as in Liker *et al.* (2008) from digital aerial photographs. In short, vegetation cover, building density, and the presence of roads were scored for 100 cells of a 1 km^2 area around each capture site. For each site we calculated urbanization score by extracting the first principal component from a principal component analysis (PCA) of five urbanization measures (mean building density, number of cells with high building density, number of cells with road, mean vegetation density, number of cells with high vegetation density; see Table III. 1.). The PCA extracted one component with >1 eigenvalue that accounted for 92.2% of the total variance and correlated strongly (component loadings ≥0.90) with reduced vegetation density and increased densities of buildings and roads (Table III.1). We used this principal component as measure of urbanization in the analyses.

For each analysis, we chose study sites that represent independent local populations, i.e. are sufficiently far from each other to prevent significant exchange of birds between them (Table III.1). The house sparrow is a very sedentary bird: dispersal distances are typically 1–2 km (reviewed by Anderson 2006) and movements in the non-breeding season are usually <500 m (Liker *et al.* 2009; Vangestel *et al.* 2010). Distances between our capture sites ranged 1–263 km; note that even the closest study sites can differ considerably in the birds' body size and mass (Liker *et al.* 2008) with very little movement of birds between them (Liker *et al.* 2009b).

2.2. Body condition measurements

We captured house sparrows in differently urbanized habitats in Hungary between 1997–2009 using mist-nets (Table III.1). For all birds we measured tarsus length (± 0.1 mm) and body mass (± 0.1 g) upon capture, whereas other measurements were taken from various subsets of birds as described below. All capture procedures were in accordance with the relevant Hungarian laws and licensed by the local authorities (permission numbers: 847/3/2003, 9135/2004, 2255/2008).

2.2.1. Physiological indices

We captured 132 sparrows in 2009 in the end of the non-breeding season (January–March) at 12 sites and 157 birds in the molting season (September–October) at 10 sites (Table III.1). In the winter, birds were sampled for corticosterone assay by taking up to 150 µl blood within 3 minutes from capture. Because sparrows usually hit the net in flocks, we could sample corticosterone only for some of the captured birds. Within this short time frame (156 ± 4 sec) corticosterone concentrations did not increase with handling time in our sample (slope ± SE = 0.006 ± 0.025, r=0.13, P=0.886, N=35; P obtained by permutation test using the 'coin' package of R; R 2.11.0, R Development Core Team 2010), so we refer to these as "baseline" (Wingfield 1994; Romero & Reed 2005). These birds were then kept in a cloth bag for 30 minutes, after which a second blood sample was taken from the other wing to measure the level of corticosterone induced by acute stress (capture-restraint protocol; Wingfield 1994). In house sparrows, corticosterone concentrations are maximal 30 minutes after the initial stressor (Romero & Romero 2002). As the amount of blood required for corticosterone assay is relatively large for sparrows, we did not take any more blood from birds sampled for corticosterone. From the rest of the captured birds we collected two blood samples from the brachial vein within 53 ± 1.75 minutes from the time of capture: up to 100 µl blood into a heparinized capillary tube for hematocrit measurement, and a smear from a 1-2 µl drop of blood on a microscope slide for blood cell counts. In the molting season we took blood samples for hematocrit and smears but not for corticosterone since the latter is at very low levels during molt (Romero *et al.* 2005).

Smears were air-dried, fixed in absolute methanol, and stained with Hemacolor staining set (Merck KGaA, Darmstadt, Germany); then examined under oil immersion at 1000x magnification to count the proportion of different types of leukocytes in a total of 100 leukocytes per smear. Blood samples were stored on ice until transport to the laboratory within 8 h; they were then centrifuged for 5 min at 8000 rpm. Hematocrit was measured as the relative amount of red blood cells in total blood volume in the capillary tubes.

Table III. 1. Degree of urbanization of the capture sites and the number of birds captured at each site (datasets: a: physiological indices, b: scaled mass index, c: plumage coloration). Sites are listed in decreasing order of urbanization; "other sites" include 4 sites for which urbanization was not measured because they were too close to at least one of our study sites to be treated as independent sites for the analyses of urbanization. Sites marked with asterisk had been sampled by Liker *et al.* (2008).

Capture site	Mean vegetation density score	Mean building density score	Number of cells with road	Number of cells with high (> 50%) vegetation density	Number of cells with high (> 50%) building density	Urbanization score	Dataset (sample size)
Budapest, VI. ker. 47º30′20″ N, 19º04′01″ E	0.54	1.97	99	1	97	1.841	ab (14)
Budapest, ÁOTK campus* 47º30′17″ N, 19º04′28″ E	0.80	1.85	99	3	85	1.588	bc (20)
Székesfehérvár 47º11′22″ N, 18º24′29″ E	0.78	1.65	87	6	65	1.290	ab (27)
Budapest, Lurdy Ház 47º28′08″ N, 19º04′48″ E	0.71	1.21	70	8	40	0.864	abc (14)
Veszprém, Hotel 47°05´29″ N, 17°54´43″ E	1.03	1.15	93	11	37	0.812	abc (21)
Budapest, Kőbánya-Kispest 47°27´43″ N, 19°09´00″ E	1.15	1.33	98	19	37	0.811	abc (22)
Budapest, Zoo* 47º31′11″ N, 19º04′58″ E	1.16	1.25	87	22	39	0.706	bc (55)
Várpalota 47º12′05″ N, 18º08′22″ E	1.13	1.16	95	15	19	0.634	ab (10)
Csepel 47º24′22″ N, 19º04′49″ E	1.18	1.17	80	18	23	0.533	abc (18)
Veszprém, PE campus* 47º05′12″ N, 17º54′07″ E	1.34	1.20	84	35	29	0.448	abc (105)
Veszprém, Cholnoky 47°05´15″ N, 17°55´36″ E	1.41	0.77	56	49	13	-0.107	abc (13)
Veszprém, Zoo* 47º05′32″ N, 17º53′43″ E	1.80	0.75	58	80	17	-0.415	bc (1123)
Dunakeszi, Alag* 47º37′12″ N, 19º08′55″ E	1.96	0.69	56	86	8	-0.616	b (301)
Nemesvámos 47°03´16″ N, 17°51´52″ E	1.71	0.49	27	75	11	-0.682	bc (56)
Hajmáskér 47°08´14″ N, 18°00´15″ E	1.88	0.25	41	88	0	-0.904	abc (21)
Salföld 46°50´14″ N, 17°32´57″ E	1.84	0.17	27	84	1	-0.975	ab (31)
Üllő, Dóramajor* 47º20′43″ N, 19º19′16″ E	1.97	0.35	26	97	1	-1.045	abc (248)
Bánd 47°07´17″ N, 17°47´34″ E	1.95	0.16	29	95	0	-1.082	ab (12)
Szentgál 47°06´08″ N, 17°42´20″ E	2.00	0.03	20	100	0	-1.236	ab (26)
Hortobágy, Nyugati Fogadó* 47º35′24″ N, 20º51′15″ E	2.00	0.11	14	100	0	-1.245	bc (36)
Vilmapuszta 47°05´05″ N, 17°52´03″ E	2.00	0.06	0	100	0	-1.352	ab (9)
Other sites							b (163)

For corticosterone measurement, blood plasma was extracted and kept at -20 °C until radioimmunoassay at the Centre d'Études Biologiques de Chizé following the protocol that was validated for house sparrows (Lendvai *et al.* 2011). Briefly, total plasma corticosterone was measured in samples (25µl) after ethyl-ether extraction by radioimmunoassay using a commercial antiserum. Duplicate aliquots of the extracts were incubated overnight at 4°C with 3H-Corticosterone and antiserum. Bound and free corticosterone was separated by adding dextran-coated charcoal. After centrifugation, the bound fraction was counted in a liquid scintillation counter. Two assays were run, intra-assay and inter-assay coefficients of variation were 4.67% and 5.35%, respectively, for N=6 duplicates of reference samples. Minimal detectable corticosterone levels were 0.52 ng/ml (lowest measurement: 1.47 ng/ml). Pooled plasma of different house sparrows produced a dose–response curve that paralleled the corticosterone standard curve.

In the molting season, for each bird we recorded the stage of molt (the number of freshly molted primaries), and we assigned them into one of two age classes: "young" (first-year juveniles that fledged late in the season and had remnants of nestling plumage) and "older" (birds with completed molt, including both juveniles fledged early in the season and adults older than one year). In the wintering season, the age of the birds could not be determined; by that time all birds were considered as adults.

2.2.2. Scaled mass index

To quantify the birds' body mass relative to their body size, we calculated the scaled mass index following Peig and Green (2009, 2010). This index adjusts the mass of all individuals to that which they would have if they had the same body size, using the equation of the linear regression of log-mass on log-length estimated by type-2 (standardized major axis; SMA) regression. For the calculation of this equation, we used the body mass and tarsus length data of 2345 adult sparrows from 30 sites, captured throughout the year between 1997–2009 (Table III.1). Note that this dataset partially overlaps with the one used by Liker *et al.* (2008), however, in that study type-1 regression residuals were analyzed which is a less reliable index of body condition because it underestimates the true mass~length slope and thus the residuals are systematically biased towards larger individuals (Peig & Green 2009, 2010). After excluding 13 outliers (i.e. |standardized residual| > 3), the regression slope was 1.71, whereas average tarsus length was 19 mm. Thus we calculated the scaled mass index as body mass $\times (19 / \text{tarsus length})^{1.71}$ (Peig & Green 2009, 2010). We chose tarsus length as the proxy for skeletal body size as this measure had been routinely taken during our captures. Wing length (± 1 mm) and bill length (± 0.1 mm) were measured for smaller subsets of birds; we used these data to verify our scaled mass index (see Results of this Chapter).

2.2.3. Plumage coloration

Bib size of 314 males was measured by a single person at seven sites between 1997–2008 (Table III.1). The maximum length and width of the bib was measured by ruler to the nearest mm, and bib size was calculated following Veiga (1993). This estimate of bib size is highly repeatable (Liker & Barta 2001). We used data only from November to April each year to exclude birds from the molting season (we had no comparable data for most study sites from the breeding season). We repeated the analysis of bib size using a smaller sample of males (N=89) whose bib size was measured from digital photographs (see below), but since we obtained qualitatively identical results (i.e. no relationship with urbanization; see below), here we report results only for the larger sample (i.e. bib size measured by ruler).

Wing bar size was measured in 89 males and 80 females captured at 10 sites between 2007–2009 (Table III.1) from digital photographs as described in Bókony *et al.* (2006) and Bókony *et al.* (2008). The photos were taken between November–March (i.e. only non-molting birds were photographed) and measured by a single person with very high repeatability (R=0.95, 95% confidence interval: 0.82–0.99, $F_{9,10}$=38.6, P<0.001) *sensu* Lessells and Boag (1987) using ScionImage software (see Bókony *et al.* 2006, 2008). As indicators of age, we measured wing length and tail length (± 1 mm; Selander & Johnston, 1967; Nakagawa & Burke 2008) and male mask size, i.e. the maximum length of the black mask on one side of the face (± 0.1 mm; Nakagawa & Burke 2008).

2.3. Data analysis

Measures of body condition were analyzed in linear mixed-effect (LME) models that contained capture site as random factor to control for the non-independence of individuals captured at the same site. Full models of corticosterone levels included urbanization (i.e. the principal component score), sex, date (number of days since 1 September i.e. the peak of molting season each year), and time of day (number of minutes since 7:00 each day) as predictors (i.e. fixed effects). Because preliminary analyses of baseline corticosterone revealed heterogeneity in the variances between the sexes, we used a constant variance structure (‘varIdent’ function in R) that allows for different variances in males and females. Full models of hematological indices (i.e. hematocrit and H:L ratio) included urbanization, sex, date, time of day, handling time (number of minutes from capture until blood sampling) and, for the molting season, age and molting stage (note that since the latter variables were only available for the molting season and not for winter, data from the two seasons were analyzed separately). The full model of the scaled mass index included urbanization, date, time of day, sex, and age (i.e. juvenile or adult); juveniles captured in May–September were omitted from this analysis because young birds might not finish growth until October (MacLeod *et al.* 2006). Full models of plumage coloration included urbanization, date and, for wing bar size, sex. Since the body size of sparrows is known to be related to urbanization (Liker *et al.* 2008), we controlled for body size in the analyses of bib size and wing bar size by including body mass into the full models and retaining this predictor throughout all steps of model reduction (see below). Each full model also included all 2-way interactions between urbanization and the other predictors. All models were checked for linearity by inspecting diagnostic graphs of residuals and fitted values; in no case did these indicate a non-linear relationship between urbanization and body condition indices.

As our research question was whether habitat urbanization has a considerable effect on the body condition indices, we preferred the frequentist (i.e. null-hypothesis testing) paradigm over the information-theoretic approach during our analyses for the following reasons. First, frequentist methods provide well established, efficient statistical tests for bivariate comparisons (Richards *et al.* 2011). Second, in the case of multivariate analyses, our goal was to infer the effect of urbanization while controlling for potentially confounding variables, rather than to compare the relative importance of all initially considered predictors. The inference yielded by the information-theoretic method depends critically on the set of candidate models chosen (Hegyi & Garamszegi 2011); how the potentially confounding variables interact to influence each index of body condition is beyond both our knowledge and the scope of this study. Therefore, we handled our multivariate models in the following way. We reduced each full model stepwise by excluding the confounding variable with the highest p-value in each step until only $P<0.05$ predictors remained; we inspected the models in each step and never excluded our predictor of interest, i.e. urbanization. The aim of this process was to increase the accuracy of effect size estimates for urbanization since effect sizes in full models are usually inaccurate due to noise terms (Hegyi & Garamszegi 2011). Note that our final models yielded qualitatively the same conclusions as the full models (i.e. when no stepwise selection was done). We present effect size estimates (Cohen’s *d*) with 95% confidence intervals for the variables retained in the final models, mean ± SE for bivariate comparisons and two-tailed p-values throughout the paper. All statistical analyses were performed in the R computing environment (R 2.11.0; R Development Core Team 2010), using the ‘nlme’ and ‘smatr’ packages. Sample size of each analysis is given in Table III.2.

Table III. 2. Final LME models of body condition indices. Urbanization was retained in each model during model reduction, and body mass was retained in the models of bib size and wing bar size; other predictors were excluded if they had *P*>0.05.

	***N* (birds; sites)**	**Intercept ± SE**	***b* ± SE**	***P***	**Cohen's *d* (95% CI)**
Corticosterone levels (ng/ml)					
Baseline	37; 9	3.47 ± 0.34			
sex (male vs. female)			3.19 ± 0.89	0.001	1.23 (0.49; 2.10)
urbanization			0.05 ± 0.41	0.903	0.04 (-0.64; 0.73)
Stress-induced	35; 9	43.37 ± 1.60			
urbanization			-1.80 ± 2.10	0.418	-0.30 (-1.03; 0.40)
Hematocrit (%)					
Winter	85; 12	57.40 ± 0.54			
urbanization			0.08 ± 0.61	0.896	0.03 (-041; 0.47)
Molting season	147; 10	74.07 ± 10.88			
molt stage			0.66 ± 0.19	<0.001	0.59 (0.26; 0.94)
date			-0.11 ± 0.04	0.039	-0.43 (-0.77; -0.10)
age (older vs. young)			0.004 ± 0.82	0.997	0.001 (-0.33; 0.33)
urbanization			0.48 ± 0.47	0.346	0.17 (-0.16; 0.50)
age × urbanization			-1.15 ± 0.54	0.035	-0.36 (-0.70; -0.03)
H:L ratio					
Winter[1]	41; 8	0.22 ± 0.12			
handling time			0.005 ± 0.002	0.061	0.63 (-0.02; 1.34)
urbanization			0.009 ± 0.083	0.922	0.03 (-0.61; 0.68)
Molting season	144 ; 10	0.16 ± 0.05			
handling time			0.002 ± 0.001	0.011	0.43 (0.10; 0.78)
urbanization			-0.06 ± 0.02	0.019	-0.50 (-0.84; -0.16)
Scaled mass index	1695; 21	28.49 ± 0.19			
date			-0.002 ± 0.001	<0.001	-0.17 (-0.27; -0.08)
time of day			0.003 ± 0.001	<0.001	0.38 (0.28; 0.48)
sex (male vs. female)			-0.39 ± 0.10	<0.001	-0.19 (-0.29; -0.10)
urbanization			-0.22 ± 0.16	0.205	-0.07 (-0.16; 0.03)
Body mass	1695; 21	28.50 ± 0.15			
date			-0.003 ± 0.001	<0.001	-0.21 (-0.31; -0.11)
time of day			0.003 ± 0.001	<0.001	0.42 (0.32; 0.52)
sex (male vs. female)			-0.68 ± 0.09	<0.001	-0.37 (-0.47; -0.27)
urbanization			-0.76 ± 0.12	<0.001	-0.30 (-0.40; -0.20)
Tarsus length	1809; 21	19.02 ± 0.04			
sex (male vs. female)			-0.13 ± 0.04	<0.001	-0.17 (-0.26; -0.08)
urbanization			-0.23 ± 0.04	<0.001	-0.25 (-0.34; -0.16)
Bib size (mm^2)	314; 7	179.99 ± 43.74			
date			0.27 ± 0.07	<0.001	0.42 (0.19; 0.65)
body mass			4.03 ± 1.44	0.006	0.32 (0.09; 0.55)
urbanization			1.95 ± 6.22	0.766	0.04 (-0.19; 0.26)
Wing bar size (mm^2)	169; 10	46.14 ± 40.80			
date			0.13 ± 0.07	0.048	0.31 (0.01; 0.62)
sex (male vs. female)			68.27 ± 4.28	<0.001	2.49 (2.03; 3.01)
body mass			-0.61 ± 1.37	0.655	-0.07 (-0.38; 0.23)
urbanization			-0.70 ± 2.79	0.809	-0.04 (-0.35; 0.27)

[1] Excluding the marginally non-significant effect of handling time, the final model contains only urbanization: *b* ± SE = 0.084 ± 0.096 (intercept: 0.385 ± 0.071), *P*=0.410, Cohen's *d* (95% CI) = 0.27 (-0.34; 0.90), *N*=45 birds from 9 sites.

3. RESULTS

3.1. Physiological indices

Corticosterone levels of wintering birds were not related to habitat urbanization either in baseline or stress-induced blood samples (Table III.2).

Hematocrit was significantly higher in winter (57.2 ± 0.4 %) than in the molting season (50.6 ± 0.3 %; t_{230}=14.55, *P*<0.001). Hematocrit was unrelated to urbanization in winter (Table III.2), whereas in the molting season we found a significant interaction between urbanization and age (Table III.2). In young birds, rural individuals tended to have lower hematocrit than urban individuals, whereas older adults showed the opposite trend (Fig. III.1a); thus hematocrit increased with age in rural but not in urban birds (Fig. III.1a).

H:L ratio was significantly higher in winter (0.40 ± 0.05) than in the molting season (0.29 ± 0.02; t_{198}=2.35, *P*=0.020), and increased slightly with handling time in both seasons (Table III.2); the rate of this increase was similar in differently urbanized habitats (urbanization × handling time: p>0.109). Urbanization showed no significant relationship with H:L ratio in winter (Table III.2), whereas in the molting season rural birds had higher H:L ratio than urban birds (Table III.2). The latter difference was apparently due to older rather than young birds (Fig. III.1b) although the interaction between age and urbanization was not statistically significant (*P*=0.226).

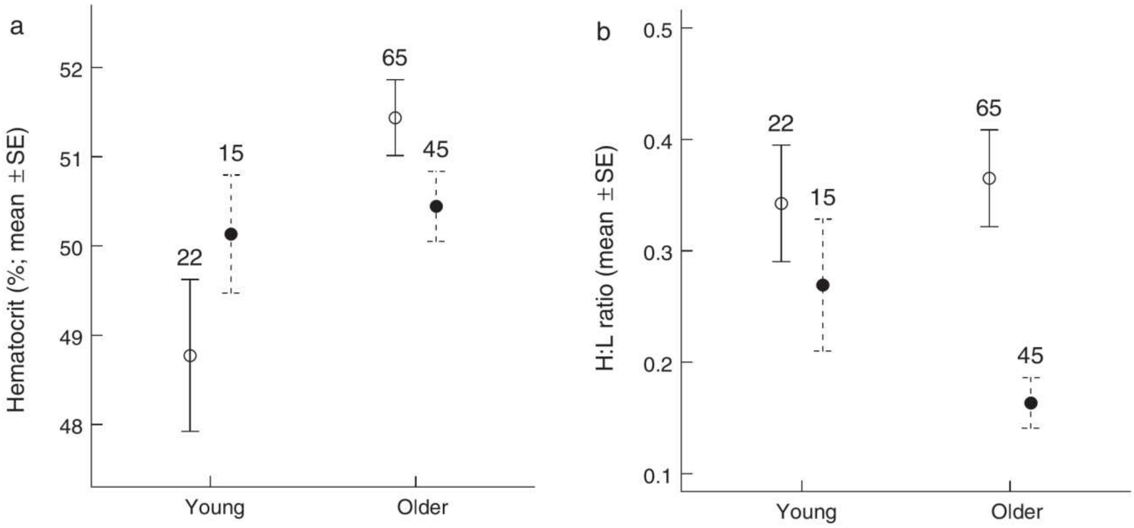

Fig. III. 1. Hematocrit (a) and H:L ratio (b) in relation to urbanization and age in the molting season. For illustrative purposes, habitat urbanization score is simplified as “rural” (negative scores; open circles) and “urban” (positive scores; filled circles). Young birds are first-year adults with remnants of juvenile plumage; older birds are adults with completed molt. Sample sizes (number of birds) are shown above each bar.

3.2. Scaled mass index

The slope of the SMA regression of log-mass on log-tarsus was similar for males and females (*P*=0.141) and for juveniles and adults (*P*=0.960). The scaled mass index was not correlated with wing length (*r*=0.03, *P*=0.198, *N*=1690) or bill length (*r*=–0.03, *P*=0.228, *N*=1401). These two lines of results imply that by calculating the scaled mass index we successfully controlled for body size differences among individuals. The scaled mass index showed no consistent relationship with urbanization (Table III.2, Fig. III.2).

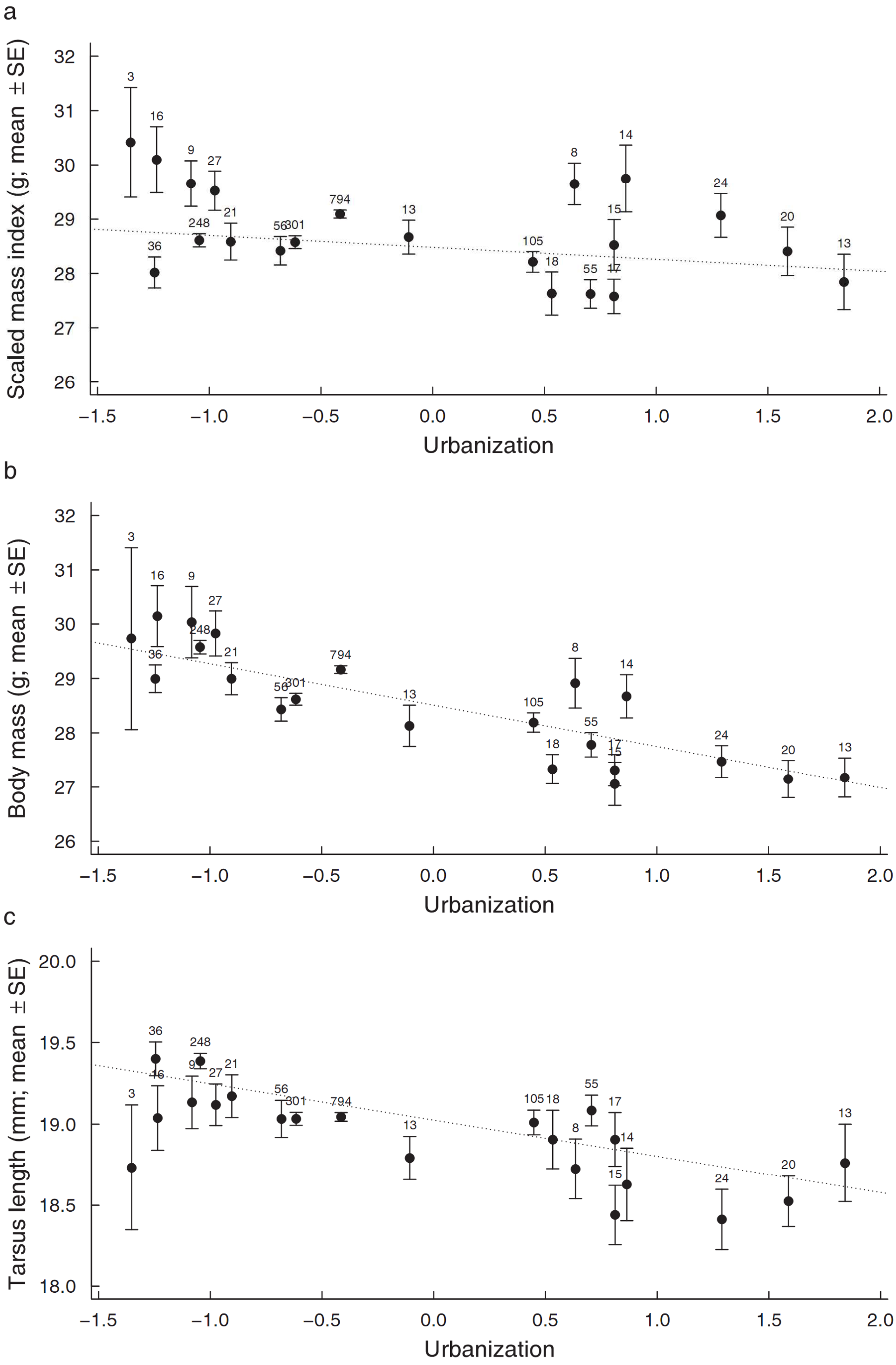

Fig. III. 2. Body mass and scaled mass index in relation to urbanization scores ranging from the least (negative values) to the most urbanized (positive values) sites. Each dot corresponds to a capture site (see Table III.1 for description of the sites). Regression lines (dotted lines) are fitted using the parameter estimates of the final LME models in Table III.2. Sample sizes (number of birds) are shown above each bar.

This was also the case when we restricted the analysis to those individuals that had been studied by Liker *et al.* (2008; slope ± SE for urbanization: -0.28 ± 0.32, *P*=0.428). In contrast, both body mass and tarsus length decreased significantly with increasing degree of urbanization (Table III.2, Fig. III.2).

3.3. Plumage coloration

Bib size and wing bar size were not significantly related to urbanization (Table III.2). We found no relationship between urbanization and any age indicator after controlling for body mass by partial correlations (male mask size: *r*=–0.16, *P*=0.886, *N*=85; male wing length: *r*=–0.03, *P*=0.632, *N*=311; female wing length: *r*=0.13, *P*=0.379, *N*=45; male tail length: *r*=0.02, *P*=0.907, *N*=60; female tail length: *r*=–0.001, *P*=0.993, *N*=44).

4. DISCUSSION

Several negative effects of ongoing urbanization can be expected to manifest in the body condition of house sparrows, such as increasing pollution or decreasing availability of human waste as food resource (Summers-Smith 2003; Shaw *et al.* 2008). Despite these expectations, we found no evidence that habitat urbanization was affecting adult sparrows' physiological or morphological condition. This study integrates a decade of investigations in various habitats along the urbanization gradient at several life-history phases, utilizing several potential indices of body condition. Out of these indices, only H:L ratio and only in the molting season showed a consistent relationship with the degree of habitat urbanization, unexpectedly indicating better condition in more urbanized habitats. This latter result, combined with the lack of habitat differences in the rest of our analyses, suggests that urbanization is unlikely to have a general negative effect on the well-being of adult house sparrows.

Individuals in poor body condition, such as those suffering from starvation or pollution, often circulate chronically elevated levels of glucocorticoids (Romero 2004; Wikelski & Cooke 2006). Beside reflecting the current health state of the individual, baseline glucocorticoid concentrations can also predict (or even determine) later fitness; for example, house sparrows with lower baseline corticosterone in the pre-breeding season produce more fledglings during the breeding season (Ouyang *et al.* 2011). Thus our finding that sparrows across the urbanization gradient had similar levels of baseline corticosterone at the end of the wintering season (on average at the same time as in Ouyang *et al.*'s study) suggests not only that they were in similar physiological condition but also that they might have had similar prospects for reproductive investment. Acute stress-induced levels of glucocorticoids are more difficult to compare among populations, as chronic stress may either enhance or attenuate the stress response (Romero 2004); furthermore, a few studies imply that animals may have adapted to urbanization by reduced stress-responsiveness (Partecke *et al.* 2006b; Fokidis *et al.* 2009). Our result that urban and rural sparrows mounted similar stress responses does not fit either scenario, suggesting that adult sparrows may perceive differently urbanized habitats equally stressful. In accordance with our findings, two recent studies found no difference in various corticosterone concentrations among differently urbanized sparrow populations in the non-breeding season (Fokidis *et al.* 2009; Chávez-Zichinelli *et al.* 2010). Although Fokidis *et al.* (2009) detected higher corticosterone levels in rural than in urban sparrows in the breeding season in a small sample of birds, such a comparison is potentially confounded by reproductive effort and brood value (Lendvai *et al.* 2007; Lendvai & Chastel 2008) that may well be affected by urbanization (Peach *et al.* 2008).

Similarly to corticosterone levels, hematocrit and H:L ratio showed no consistent relationship with urbanization in the winter, which is also in accordance with earlier results (Gavett & Wakeley 1986;

Fokidis *et al.* 2008). In the molting season, we obtained contradictory results, as hematocrit showed better condition in rural adults whereas H:L ratio showed the opposite; furthermore, these differences were weaker or even inverted in younger individuals. From our trans-sectional sample we can infer that hematocrit increased with age in rural but not in urban populations. Increasing hematocrit from hatching to fledging and later to adulthood seems to be the general pattern in birds (Fair *et al.* 2007), but our urban birds failed to fit this pattern. This could be a signal of impaired erythropoiesis in adults; however, the observation that young urban birds tended to have higher hematocrit than rural counterparts suggests an adaptive explanation by which individuals may preemptively circumvent the adverse conditions during early development. We believe that our hematological measurements were reasonable because they exhibited biologically meaningful relationships: the lower hematocrits of heavily molting birds (Table III.2) and the increase of H:L ratio with handling time (Table III.2) support that both measures are indicative of stress in general. Nevertheless, we might not have been able to control for all confounding effects; for example, both hematocrit and H:L ratio can be influenced by the individual's parasite load which may or may not be related to urbanization (Fair *et al.* 2007; Fokidis *et al.* 2008); e.g. the lower H:L ratio of urban birds might have been due to reduced rate of parasitic infections (Evans *et al.* 2009c). Notably, H:L ratio had by far the largest coefficient of variation (CV; 95%) among our indices of body condition (7-63%). Although hematocrit seemed less noisy (9% CV), it differed mainly among older birds, a group in which individuals might have varied greatly in their exact age from first-year up to several years. Therefore, whether habitat urbanization affects the hematological condition of molting birds in interaction with their age, and whether this effect is attributable to pathogenic infections or other stressors, requires further investigations.

Additionally, we found that neither bib size nor wing bar size varied consistently with urbanization, implying that differently urbanized populations experience similar nutritional conditions during the molting season. Although plumage coloration may be influenced by several intrinsic and extrinsic factors, these are unlikely to have confounded or biased our results concerning urbanization for the following reasons. First, age may be an important determinant of plumage coloration in sparrows (Nakagawa & Burke 2008), however, plumage traits such as male mask size, wing length and tail length that all increase with age in sparrows (Selander & Johnston 1967; Nakagawa & Burke 2008) showed no indication that urbanization alters the age structure of populations. Second, both bib size and wing bar size may be subject to sexual selection, the strength of which may differ between differently urbanized habitats e.g. due to competition for differently available nesting sites (Yeh 2004; Price *et al.* 2008). However, the final model for wing bar size did not include the interaction term between urbanization and sex, suggesting that the degree of sexual dimorphism, a proxy for the strength of sexual selection, was not related to habitat urbanization across our study sites. Furthermore, a recent meta-analysis found very little evidence for sexual selection currently acting on bib size (Nakagawa *et al.* 2007). Although bib size signals dominance status in male sparrows (Nakagawa *et al.* 2007), previous results on competitive behaviors suggest that there is no considerable difference in the intensity of competition between urban and rural populations (Bókony *et al.* 2010). Thus, our result that neither bib size and nor wing bar size varies systematically along the urbanization gradient is in agreement with the repeated finding that urban and rural sparrows retain their differences in body mass even when receiving the same diet under identical captive conditions (Liker *et al.* 2008; Bókony *et al.* 2010), implying that adult sparrows are unlikely to face different nutritional conditions at differently urbanized habitats.

The most frequently applied index of body condition in animal ecology studies is body mass corrected for body size, which can express the amount of energy reserves such as fat and muscle and thereby reflect nutritional state (Peig & Green 2009, 2010). When this index was calculated as residual body mass from type-1 (ordinary least-squares, OLS) regression with tarsus length, it showed a negative relationship with the degree of habitat urbanization (Liker *et al.* 2008). However, this method has several drawbacks (Peig & Green 2009, 2010); therefore, here we re-evaluated this analysis by using a more reliable measure of body condition, the scaled mass index, and extending the earlier dataset by 14 additional capture sites, summing up to more than one and a half thousand individuals. While this revised and extended study corroborated the previous result that sparrows' body mass is reduced in more urbanized habitats (Liker *et al.* 2008), we found no consistent relationship between urbanization and the scaled mass index. Furthermore, the final model did not include the interaction term between urbanization and date, suggesting that the scaled mass index of adult sparrows did not differ among differently urbanized habitats at any time of the year, i.e. in any life-history phase after the first molt. The previously found relationship between urbanization and OLS residuals (Liker *et al.* 2008) is probably an artifact simply reflecting the smaller size of urban birds, because the OLS method inflates residuals with increasing length (Peig & Green 2009, 2010).

Therefore, our results indicate that while adult birds seem to fare comparably well in both habitats, urban individuals are considerably smaller but not leaner compared to their rural conspecifics (Liker *et al.* 2008; Bókony *et al.* 2010; this study). The smaller body size of urban birds may be a consequence of inadequate growth during early development (Peach *et al.* 2008), adaptation to predation by cats and sparrowhawks (Beckerman *et al.* 2007; Bell *et al.* 2010; ***Chapter V***), or may be an adaptive response to the urban heat island effect (Evans *et al.* 2009b) or the less fluctuating food availability of urbanized habitats may also allow smaller size. The species' lifestyle may provide explanation for adult urban sparrows' comparably fair body condition. It is known that the proportion of arthropod food is decreasing with nestling age, and older chicks consume more vegetable material, switching to primarily seed diet after independence (however, in breeding seasons, especially during egg-laying periods, the diet of adult females also contain insect food; Anderson 2006). Species with granivorous diet often show positive response to urbanization (***Chapter I***) as continuous anthropogenic food input reduces risk of starvation and may enhances adults' physical condition (Robb *et al.* 2008). Beyond communal waste and other food sources this species willingly utilize, subsidized seed in bird feeders is an especially important 'benefit' of urbanization, as bird feeding is a very popular activity in several parts of the world (Evans *et al.* 2009d).

Besides the methods applied in this study, there are other approaches to assess individual condition and measure environmental stress effects on animals. One of these is to measure fluctuating asymmetry (FA). In bilaterally symmetric animals the phenotypic deviation from the perfect left-right symmetry during development can be attributed to environmental stress (among other factors). Since this deviation is not directional at the population level (i.e. in a given trait its direction is random between individuals), it is termed 'fluctuating' asymmetry; its statistical mean (i.e. left minus right values of the given trait) is zero and its variation is normally distributed around zero in a population. However, increased environmental stress is suggested to enhance the levels of FA in a population, therefore populations living under different levels of stress are expected to differ in the magnitude of FA (this approach and its potential drawbacks are reviewed e.g. Graham *et al.* 2010). Vangestel (2011a) studied the relationship between the extent of FA (in tarsus and rectrix length) and nutritional stress (as reflected by ptilochronological feather marks) in free-living house sparrows of differently urbanized habitats, and found no support for any habitat-related differences in the extent of FA. This finding is in line with those of this study.

Ptilochronology (the study of feathers' growth bar size; Grubb 1989) is also an approach to detect severe environmental stress affecting an individual during its feather development. The basic assumptions of the method are (a) that dark and light growth bars are alternating according to the birds' diurnal activity (i.e. light bands are associated with reduced blood pressure during sleep, thus one pair of growth bars represents a 24 hour-period), and (b) that narrower bar sizes reflect poorer nutritional periods, i.e. hindered feather development (Grubb 2006). Vangestel (2010) also applied ptilochronology to study adult house sparrows' nutritional condition along an urban gradient in Ghent, Belgium, and reported the signs of the strongest nutritional stress in urban populations. The reason might be that urban birds' have smaller home ranges consisting of highly fragmented vegetation, as the author suggests. However, that study monitored the urban population of only one study area, thereby it lacks the potential for further generalizations and its conclusion has to be treated with caution because growth bar widths were measured on normally grown feathers for which the method is less well validated than for feathers with experimentally induced growth (Kern & Cowie 2002; Matysioková & Remes 2010).

Taken together, this study demonstrates that adult house sparrows in urbanized areas are unlikely to be in inferior body condition compared to their conspecifics in more natural habitats. Thus, this result does not support the predictions of the 'credit card hypothesis' (Shochat 2004). This theory, on the one hand, predicts overexploitation (instead of resource matching) in cities, leading urban birds to be in generally inferior body condition as a result of reduced top-down control, increased food predictability and competition in cities. Another prediction of the hypothesis, that urban populations consist mostly of poor competitors ('the losers'), was formerly disaffirmed by some results of Bókony *et al.* (2010), who compared the competitive performance of urban and rural sparrows and did not find any habitat related differences. Moreover, they did not find any relation between individual's body mass and competitive success, which also underscores my results here, that urban birds' smaller body size may not be the consequence of their inferior physical condition or poorer competitive abilities. A study (Rodewald & Shustack 2008) conducted in USA on a successful synanthropic species, the Northern cardinal (*Cardinalis cardinalis*) estimated the species' density in urban forests to be four times higher compared to rural areas, yet it did not find any significant habitat differences in annual breeding success (mean of fledged chicks per pair), apparent survival rates and body condition. These results are also contradictory to the credit card hypothesis' proposal that synanthropic species gain lower per capita resources leading to inferior condition in urban habitats.

Recent research shows that urban and rural sparrows have similar reproductive efforts in terms of clutch size and annual number of breeding attempts, but nestlings' growth and survival is reduced in urban nests (Peach *et al.* 2008; and see ***Chapter IV***). Combined with our present results that neither index of body condition supports an inferior health state of urban adults in any period of their yearly cycle, these findings imply that urbanized habitats are more likely to constitute a stressful environment for house sparrows in early developmental phases rather than in their adulthood.

Finally, the inconsistencies found between different body condition indices (Liker *et al.* 2008; this study) emphasize that drawing conclusions from a single measure of individual state can be misleading. Therefore, studies aimed at the monitoring of urban management effects on wildlife should rely on multiple approaches, taking alternative measurements in various life-history phases.

CHAPTER IV

Urbanization, nestling growth and reproductive success in a moderately declining house sparrow population

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ABSTRACT

Ecological conditions are likely to change with increasing urbanization, influencing the demography and size of animal populations. Although being one of the most tightly linked species to humans, the house sparrow has been suffering a significant decline worldwide, especially in European cities. Several factors have been proposed to explain this conspicuous loss of urban sparrows, but studies evaluating these factors are usually restricted to Britain where the decline was very drastic, and it is unclear whether similar or different processes are affecting urban populations of the species elsewhere. In this study we investigated the reproductive success of urban and rural sparrows in a central European country, Hungary where our census data indicate a moderate decline during the last decade. We found that rural pairs produced more and larger fledglings than suburban pairs, and the difference remained consistent in two years with very contrasting meteorological conditions during breeding. This difference is likely explained by habitat differences in nestling diet, because we found that (1) rural parents provided large prey items more often than suburban parents, (2) birds from differently urbanized habitats produced fledglings of similar number and size in captivity under identical rearing conditions with ample food for nestlings, and (3) in a cross-fostering experiment, nestlings tended to grow larger in rural than in suburban nests irrespective of their hatching environment. These results agree with those found in a recent British study, indicating that poor nestling development and survival due to inadequate diet may be widespread phenomena in urbanized habitats.

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1. INTRODUCTION

The house sparrow became one of the most widespread and abundant avian species by following man throughout the world (Anderson 2006). Despite this historical success, the species has been declining since the early 1980's at several parts of the globe, including many countries across Europe (Kelcey & Rheinwald 2005; Murgui & Macias 2010; Kekkonen *et al.* 2011), North America (Erskine 2006; Lowther 2006), Australia (Olsen *et al.* 2003) and India (Ghosh *et al.* 2010). This phenomenon is especially well documented in Britain where the most drastic declines have been detected, particularly in urbanized areas (Robinson *et al.* 2005; De Laet & Summers-Smith 2007). As a result, the house sparrow is now listed as a species of conservation concern in Europe (SPEC category 3) and of special conservation concern (Red List) in Britain (Baillie *et al*. 2009).

As the timing and rate of decline was found to differ between rural and urbanized populations (Chamberlain *et al*. 2005; Robinson *et al.* 2005; Erskine 2006), it has been suggested that different mechanisms are driving population trends in different habitats with respect to urbanization (De Laet & Summers-Smith 2007; Shaw *et al.* 2008). Studies of rural populations in Britain suggested that reduced annual survival is likely to be responsible for the decreasing trends in farmland areas, probably because recent changes in agricultural practices limit the availability of food supplies for wintering sparrows (Crick *et al.* 2002; Hole *et al.* 2002). In contrast, suburban sparrows were found to experience higher nest failure rates (Crick *et al*. 2002) mostly due to reduced nestling survival (Peach *et al.* 2008) compared to their rural counterparts in Britain, thus decreased reproductive success has been suggested to account for the decline of urbanized populations. These studies indicate that investigating demographic differences between habitats may help us understand the effects of changes in land use and urbanization, and might also shed light on the causes of population decline.

Several reasons have been proposed for the reproductive failure of urban sparrows. First, nestlings require an arthropod diet, and parents may be unable to find nestling food of sufficient quantity and/or quality due to the scarcity of native vegetation. Recent development of cities often results in losses of green space such as gardens being replaced by paved parking lots (Shaw *et al.* 2008), and even existing vegetation may harbor poor insect fauna if it consists mainly of exotic or evergreen plants (Southwood 1961). Supporting this view, a study in and around the city of Leicester, Britain found that the survival of sparrow nestlings correlated negatively with high amounts of vegetable material in their diet and positively with high abundance of aphids around the nest (Peach *et al*. 2008). Second, arthropod density may be reduced in cities by environmental pollution, especially traffic emissions (Summers-Smith 2007). Although the effects of traffic-related air pollutants on animals are not well understood, they may affect invertebrates (Raupp *et al.* 2010; Zvereva & Kozlov 2010); furthermore, they might also have direct adverse impact on vertebrates such as the nestlings and adults birds (Eeva *et al.* 2003; Swaileh & Sansur 2006). The Leicester study also found reduced nestling growth in areas with high nitrogen-dioxide air pollution (Peach *et al.* 2008). Third, urban parents may suffer increased mortality by collisions with vehicles (Heij & Moeliker 1990) or predation by the growing numbers of domestic cats (Woods *et al.* 2003) and urbanizing raptors (Bell *et al.* 2010). Moreover, increased predator density may reduce the breeding success of house sparrows via indirect, sub-lethal effects such as decreased foraging efficiency (Beckerman *et al.* 2007) and impaired reproductive capacity due to physiological stress (Boonstra *et al.* 1998).

Each of the above hypotheses has received some correlational evidence recently (Peach *et al.* 2008; Shaw *et al.* 2008; Bell *et al.* 2010), thus it is possible that the combination of several factors is responsible for the urban declines of house sparrows. However, it is yet unclear which of these factors have the largest effects. As detailed above, either parents or nestlings or both may be negatively affected by increasingly urbanized environments; separating these effects should help to focus conservation efforts (i.e. by identifying whether adults or young should be protected more, and whether from predators or from food shortage). Furthermore, the extent and causes of house sparrow population declines have been studied in much greater detail in Britain than elsewhere (Crick *et al.* 2002; Hole *et al.* 2002; Peach *et al.* 2008; Shaw *et al.* 2008), therefore it is difficult to assess whether the dramatic British decline is a special case or rather represents a more general trend in Europe or even worldwide. To our knowledge, no comparative study of urban and rural house sparrows' breeding success or survival has been conducted outside Britain after the onset of population declines, yet such studies would be of crucial importance for assessing whether the potential mechanisms and conservation recommendations identified in Britain are relevant for protecting the species in the rest of its range.

In the present study, our aims were four-fold. First, we assessed the status of the house sparrow population in a Central European country, Hungary by studying temporal trends between 1999 and 2011. Second, we investigated the species' breeding success and nestling growth in differently urbanized habitats. Third, we observed the parents' chick-feeding behavior to compare the quantity and quality of nestling food between habitats. Finally, we conducted two experiments to assess the importance of environmental conditions during nestling development. In a common garden experiment we allowed adult sparrows from urban and rural sites to reproduce in the same environment in captivity, to see if they show any difference in parental qualities. If urbanization exerts long-term negative effects on adult birds (e.g. infertility, maternally derived toxins), we expect these to manifest in the common environment as well. In the second, cross-fostering experiment we swapped few days-old nestlings between suburban and rural nests, thereby separating genetic and pre-natal environmental effects from those of the rearing environment. If urbanization mainly affects nestlings by the actual environmental conditions (e.g. diet) experienced between hatching and fledging, we expect nestling growth to be influenced by rearing habitat to a greater extent than by birth habitat.

2. METHODS

2.1. Population trends

Data for the analysis of population trend of the house sparrow in Hungary were collected by the Hungarian Common Bird Monitoring Scheme (MMM; Szép & Gibbons 2000). MMM is a country-wide monitoring scheme in which ca. 1000 participating observers carry out 5 minutes double point counts during the breeding season (15th April - 10th May, and 10th May - 10th June) at 15 randomly selected, 100 m radius observation points situated in semi-randomly selected 2.5×2.5 km UTM squares (Szép & Gibbons 2000). This monitoring scheme has been running since 1999 in Hungary, with on average 150-300 UTM squares being surveyed yearly. The sampled areas cover the country and the distribution of the main habitat types in the sampled areas is similar to the country total (Szép & Nagy 2002). For the trend analysis only those observations are considered which meet the standard protocol of the field survey, i.e. the observer was able to identify the species, observations took place between 5-10 a.m. in two days separated by at least two weeks in the given season, and there was no rain or strong wind during the census (Szép & Gibbons 2000). For the house sparrow, 262 UTM squares were surveyed between 1999-2011. We analyzed these count data by the TRIM software (Pannekoek & Strien 2001, http://www.ebcc.info/trim.html), an efficient implementation of Poisson regression to analyze time-series of count data collected at many sites with imputing missing data, and to produce indices and associated standard errors that describe the changes in population size relative to a reference census (population estimate for the first year).

Sites included to the national monitoring scheme do not overlap with the localities we used for studying breeding success (see below), therefore we do not have population trend estimates for our specific study sites. Nevertheless, as a proxy for trends in local population size, we provide annual data on nest box occupancy (% of available nest boxes in which sparrow breeding was recorded) and total number of fledglings (see below) between 2005-2010 for our suburban site (we do not have comparable data for rural sites).

Table IV.1. Characteristics of the study sites (in order of decreasing degree of urbanization) for each dataset (F: reproduction and nestling growth in the field, CG: common garden experiment, CF: cross-fostering experiment).

Study site	Mean vegetation density score	Mean building density score	Number of cells with road	Number of cells with high (> 50%) vegetation density	Number of cells with high (> 50%) building density	Data set
Budapest, Kőbánya-Kispest 47°27´43˝ N, 19°09´00˝ E	1.03	1.15	93	11	37	CG
Veszprém, Hotel 47°05´29˝ N, 17°54´43˝ E	1.15	1.33	98	19	37	CG
Veszprém, Zoo 47º05′32˝ N, 17º53′43˝ E	1.80	0.75	58	80	17	F, CF
Nemesvámos 47°03´16˝ N, 17°51´52˝ E	1.71	0.49	27	75	11	CG
Üllő, Dóramajor 47º20′43˝ N, 19º19′16˝ E	1.97	0.35	26	97	1	CG
Hidegkút 46°59´57˝ N, 17°49´45˝ E	1.95	0.21	18	95	1	F
Szentgál 47°06´08˝ N, 17°42´20˝ E	2.00	0.03	20	100	0	F, CF
Hárskút 47°11´09˝ N, 17°47´53˝ E	2.00	0.12	12	100	0	F
Vilmapuszta 47°05´05˝ N, 17°52´03˝ E	2.00	0.06	0	100	0	F

2.2. Reproduction, nestling growth and chick feeding in the field

We studied free-living house sparrows breeding in rural and suburban nests in 2009–2010. Rural nests were monitored at two farm sites (Szentgál and Vilmapuszta; Table IV.1, Fig IV.1) and at the edges of two small villages (Hidegkút and Hárskút; Table IV.1, Fig IV.1); these sites are characterized by high vegetation density with a few buildings and roads. Sparrows at these sites breed both in nest boxes and other available nesting sites (e.g. roofs). Suburban nests were monitored in Veszprém, in the territory of Veszprém Zoo (Table IV.1) which is situated at the edge of the town, directly connected to a residential area with mostly large blocks of houses and roads with moderate to heavy traffic. This site is characterized by more buildings and paved surfaces than the rural sites (Table IV.1) and a high level of human disturbance due to intensive daily maintenance and construction work and large visitor numbers (ca. 700-2000 people per day from April to August). Furthermore, the zoo site is similar to suburban and urban sites in that its vegetation consists mostly of ornamental, evergreen and exotic species such as

Pinus nigra. Here we studied sparrows using nest boxes; our data from earlier years at this site showed that natural and box nests did not differ in brood size (median = 3 in both types of nest, χ^2 test: χ^2_5=3.81, p=0.577, n=71 nests) or nestling size (body mass: 23.61±0.44 vs. 23.45±0.34 g, t_{222}=0.30, p=0.768; tarsus length: 18.52±0.10 vs. 18.46±0.09 g, t_{215}=0.49, p=0.625). We could not study inner-city nests because these were not accessible and urban sparrows did not occupy the nest boxes we had provided (as in Peach *et al.* 2008). The mean distance between our study sites was 12.5 ± 1.5 km in a range of 2.2–20.5 km (Fig IV.1). Given that the house sparrow is a very sedentary species (e.g. Anderson 2006, Liker *et al*. 2009, Vangestel *et al.* 2010, 2011b) our sites were supposed to be far enough from each other to prevent significant exchange of sparrows amongst them.

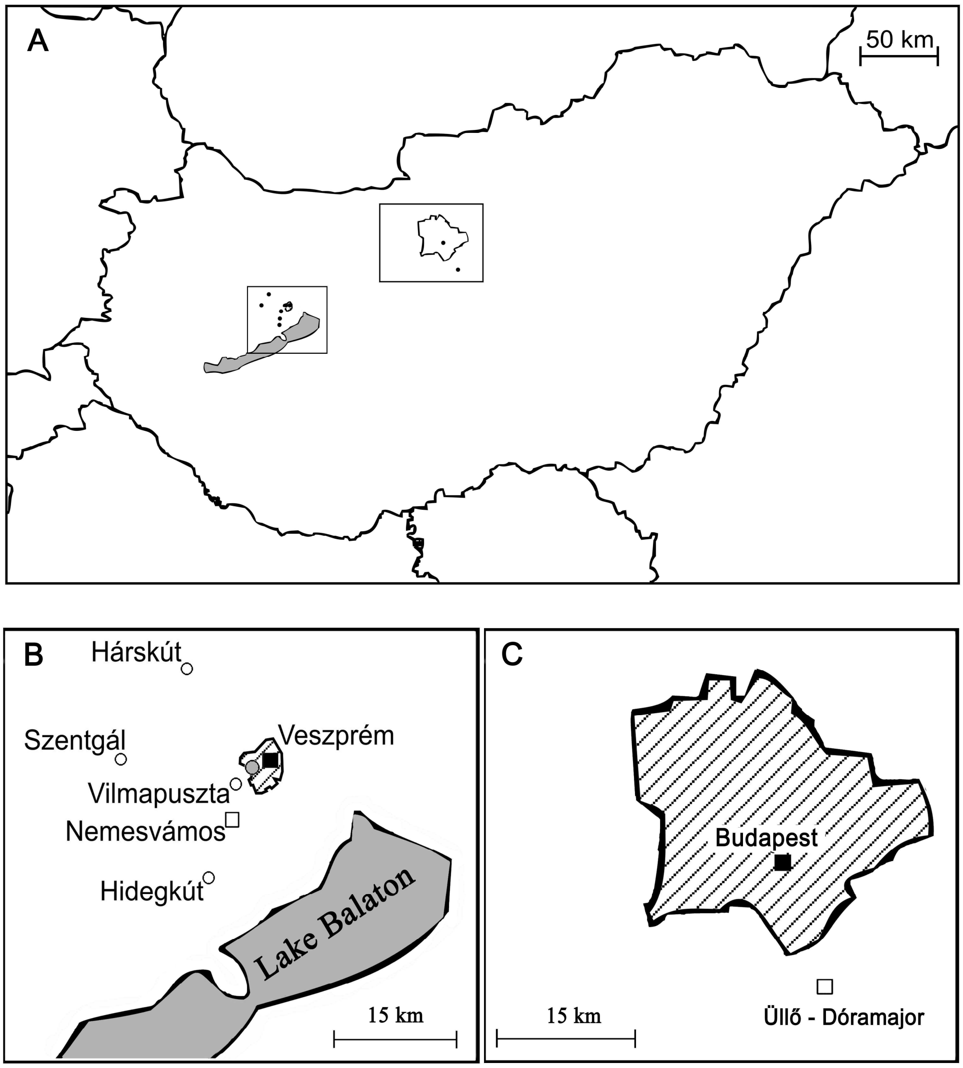

Fig. IV.1: Locations of the study sites in Hungary. Dots represent sites of the field study and cross-fostering experiment, whereas squares represent the capture sites of birds in the common garden experiment. Rural, suburban, and urban sites are marked by white, grey, and black symbols, respectively.

We verified in two ways that our suburban site represents a more urbanized habitat for house sparrows than our rural sites. First, we quantified the degree of habitat urbanization following Liker *et al.* (2008) by scoring vegetation cover, building density, and the presence of paved roads in 100 cells of a 1 km^2 area around the center of each site (Table IV.1). The number of cells with high (>50%) vegetation density was less, whereas the number of cells with roads and high (>50%) building density was higher in the suburban habitat than in the rural habitats (see Table 1; χ^2 tests: $\chi^2_1>15.74$, $p<0.001$). Second, we compared the morphology of adult birds captured in autumn with mist-nets between the Veszprém Zoo and Szentgál (i.e. the site at which 91% of our rural nests were studied). In accordance with our earlier result that sparrows are smaller in more urbanized habitats (Liker *et al*. 2008), we found that birds at our suburban site had on average 0.93±0.27 g less body mass ($t_{1023}=3.49$, $p<0.001$) and 1.18±1.52 mm shorter tarsi ($t_{961}=7.81$, $p<0.001$) than birds at the rural site.

During both years, we checked all nests regularly at least twice a week from April to August (i.e. the breeding season of house sparrows in Hungary) to record the dates of laying and hatching, and the number of eggs and chicks in the nests. We measured the body mass (± 0.1 g), tarsus length (± 0.1 mm), and wing length (± 1 mm) of nestlings when they were 8-12 days old (75% of the nestlings were measured at 9-11 days of age). Brood size at this age is a good predictor of recruitment rate in house sparrows (Schwagmeyer & Mock 2008); since disturbing nests with older nestlings can cause premature fledging, we used the number of nestlings at the time of measuring (i.e. pre-fledging age) as proxy for the number of fledglings. Nestling measurements were taken by two persons with high inter-person repeatability.

During the breeding season, weather conditions were more favorable in the 1st year as maximal daily temperatures were on average 1.91 ± 0.46 °C higher (paired t-test, $t_{152}=4.15$, $p<0.001$) and the daily amount of rainfall was 1.53 ± 0.77 mm lower (paired Wilcoxon test, $V=1583.5$, $p=0.043$) than in the 2nd year. The total amounts of rainfall in the breeding seasons were 290 mm and 525 mm in 2009 and 2010, respectively (data on weather were recorded in Veszprém between 1 April and 31 August in both years), making the latter year's breeding season unusually wet and (sometimes) cold.

In 2010-2012 we also used data on parents' chick-feeding activity from 71 broods (52 rural, 19 suburban). We conducted 1-4 surveys on each of these broods, between 8:00-15:00, at nestling age of 4-7 (in a few cases 3 or 8) days old (mean age in days was 5.97 ± 0.13 SE in rural, 5.37 ± 0.21 SE in suburban nests). We observed the nests from a distance either by spotting scope or by video-camera for 30-35 minutes, and recorded the number of visits by each parent. Also, for each visit we recorded the parent's sex, and categorized the size of the food item delivered as small, medium, large or unknown following Schwagmeyer and Mock (2008) who found that the delivery rate of large food items (enormous prey or 'e-prey') strongly predicted nestling mass and recruitment in house sparrows. For the comparision of feeding rates, we used all observations in which at least one of the parents visited the nest at least one time (193 observations: 134 rural and 59 suburban). For the study of prey size, we used only those observations in which the parent delivered at least one recognizable sized food item (i.e. small, medium or large), thus we had 137 observations (96 rural, 41 suburban) in 61 broods (44 rural, 17 suburban) in total.

2.3. Manipulations of the rearing environment

(a) Common garden experiment

To study reproductive success and nestling growth under identical environmental conditions, we brought adult sparrows from 2 urban and 2 rural sites into captivity. We captured 20 males and 20 females by mist-nets in September-October 2007 at four sites in Hungary (Table IV.1; for further details see Bókony *et al.* 2010). The mean distance between our study sites was 78.7 ± 21.6 km in a range of 4.6–117.3 km (Fig IV.1). The two inner-city sites had much less vegetation cover and higher density of roads and buildings than the two farm sites (see Table 1; $\chi^2_1>26.66$, $p<0.001$); urban birds were smaller than rural birds (Bókony *et al.* 2010). We ringed each bird with a unique combination of a numbered metal ring and three plastic color rings. We formed 4 flocks of 10 individuals: 2 groups of urban and 2 groups of rural birds. We kept urban and rural birds in separate flocks to make sure that breeding pairs are formed between members of the same habitat type (i.e. urban or rural). Each flock consisted of equal number of males and females from both sites of the respective habitat type, and we housed them in four outdoor aviaries in the Veszprém Zoo. Each aviary was ca. 3 m high and 3 × 4 m large, and contained artificial roosting trees and at least 15 nest boxes. Birds were provided *ad libitum* food (a mixture of millet, wheat, and sunflower seeds) and water with multivitamin droplets throughout the study. All captures and housing of the birds were in accordance with the relevant Hungarian laws and were licensed by The Middle Transdanubian Inspectorate for Environmental Protection, Natural Protection and Water Management (permission number: 2255/2008).

During the breeding seasons (March-August) of 2008 and 2009, birds were supplied plenty of nesting material (hay and chicken feathers) and food for the nestlings (mainly mealworms and *Diptera* larvae, occasionally amended by boiled eggs, cat food, carrots and apples). Regular observations were made to ascertain the breeding status of each individual. During the first year, birds did not start breeding until June and only 9 pairs formed, so to minimize disturbance we checked the nests only once a week and collected data only on the body mass of nestlings prior to fledging. In the second year, birds started breeding at the end of March without any sign of stress and almost all of them paired up, so we checked nests at least twice a week to monitor clutch size, date and success of hatching, and to count, ring and measure the nestlings at the standard age of 9-11 days. Nestlings were ringed similarly to adults, and their body mass, tarsus length and wing length were measured the same way as for nestlings in the field. We also recorded the parents' chick-feeding activity similarly to that of free-living birds (see above). Each nest was observed for 30 minutes from a hide 4 times: once at the nestlings' age of 4-6, 7-9, 10-12, and 13-15 days, respectively. Because captive birds were feeding their nestlings almost exclusively with the mealworms and *Diptera* larvae we had provided, we did not record the size of delivered prey during these observations.

Mortality of the captive adults was low compared to the natural annual rates of ca. 40-50% (Anderson 2006): 7 out of 40 died during the two study years. Birds in the aviaries reproduced well in terms of brood size and nestling growth (see Results). Mortality of captive young was high in the post-fledging period, similarly to the 42-92% natural rates (Anderson 2006): 13 out of 26, and only 10 out of 112 ringed nestlings survived until September in 2008 and 2009, respectively. The particularly high fledgling mortality in the second year was due to an outbreak of coccidiosis and mycoplasmal conjunctivitis which we were unsuccessful at preventing and treating by medication. Following the epidemic, however, all surviving birds were in good condition during autumn and winter 2009.

In September each year, when young had become independent of their parents, we captured and weighed them again, and moved them from their home group to the other group of the same habitat type to prevent parent-offspring inbreeding. Young birds that hatched in 2008 and survived to the next spring (n=7) were allowed to breed in 2009. In spring 2010, all birds were released at their site of capture; captive-reared birds were released along with their familiar flock-mates.

(b) Cross-fostering experiment

In 2010, we conducted a field experiment in which we swapped hatchlings between rural (Szentgál) and suburban (Veszprém Zoo) nests (distance between the sites was 15.2 km). We chose pairs of rural and suburban broods that hatched on the same day (± 1 day), and we swapped half of the broods between them 0-3 days after hatching (if brood sizes were different, half of the smaller brood was swapped with the same number of hatchlings from the other brood). To mark each hatchling individually, we applied paint markings (Deco Painter, Marabu Co., Germany) and small plastic bands on their legs. When the nestlings reached the age of 9-11 days, we measured their body mass, tarsus length and wing length as described above.

Due to the adverse weather conditions of 2010, breeding attempts were few and poorly synchronized, so we could swap hatchlings only between 8 pairs of nests (30 hatchlings were swapped, 39 hatchlings remained in their home nest), and 1 suburban and 4 rural broods died completely before reaching the age of 9-11 days. The resulting small sample size precluded powerful statistical analyzes; therefore we only report the mean ± SE measurements of nestling growth without statistical tests. Broods and nestlings involved in this experiment were not included in any analysis of reproductive performance and nestling growth of free-living birds.

2.4. Data analysis

Measures of breeding success were analyzed in generalized linear mixed-effects (LME) models that contained nest site ID as a random factor to control for the potential non-independence of subsequent broods at a given nest site (as these often belong to the same pair). We used Poisson distribution in models of clutch size and brood size, and binomial distribution in models of hatching success (i.e. the proportion of eggs hatched, for all nests in which incubation had started) and fledging success (i.e. the proportion of hatched nestlings that were alive at the age of 9-11 days, for nests that hatched at least one nestling); Pearson's goodness of fit tests indicated no overdispersion in any of these models ($p>0.753$). As predictors, we included habitat (i.e. suburban or rural), year, and date (number of days since 1 April i.e. the start of breeding season each year). The number of broods raised successively in a given nest box or nest site was used as an estimate for the annual number of broods raised per pair (Peach *et al.* 2008); this variable was analyzed in a generalized linear model with Poisson distribution (dispersion parameter = 0.29) including habitat and year as predictors. Measures of nestling size were analyzed in LME models that contained nest site ID and brood ID as nested random factors to control for the non-independence of nestlings within a given brood. The models included habitat, year, date, identity of the measuring person, brood size and nestling age at the time of measuring as predictors.

For each feeding surveys we calculated the 'e-prey' rate as the number of delivered large food items divided by the number of all certainly recognized food items (i.e. we excluded parental feeding visits of 'unknown' category). 'E-prey' rate was analysed in generalized LME models with quasibinomial distribution that contained nesting site (derived from the year and nest site ID) and brood as random factors. The initial model included year, date, time of day, length of the observation, number of nestlings, age of nestlings, sex of the parent and habitat (i.e. suburban or rural) as predictors. Chick-feeding rates were calculated as the number of parental visits to the nest divided by the number of nestlings, and analyzed by LME with Poisson distribution with the same predictors and random factors as in the above 'e-prey' rate model. The model included year, date, time of day, length of the observation sex of parent, and habitat as predictors and nest site ID as a random factor (i.e. male and female feeding rates at the same nest were treated as repeated measures).

Data from the common garden experiment were analyzed similarly to the data of field nests, except that pair ID was used instead of nest site ID as a random factor since the identity of pairs was known in these cases. In the analysis of chick-feeding rates we also included the interaction of nestlings' age and parent's sex as data on age were collected throughout the entire nestling period and because that the feeding rate of males and females are known to vary differently with brood age in house sparrows (Anderson 2006). When testing the effect of habitat (i.e. rural or urban origin of breeding birds), we could not control for potential differences between aviaries because urban and rural birds were kept in different aviaries; however, we found no significant differences between aviaries in any measure of reproductive success or nestling size (LME: all $p>0.163$).

Each initial model also included all 2-way interactions between urbanization and the other predictors, and the date × year interaction. We preferred the frequentist (i.e. null-hypothesis testing) paradigm over the information-theoretic approach during our analyses since our goal was to infer the effect of urbanization while controlling for potentially confounding variables, rather than to compare the relative importance of all initially considered predictors. The inference yielded by the information-theoretic method depends critically on the set of candidate models chosen (Hegyi & Garamszegi 2011); how the potentially confounding variables interact to influence each dependent variable we measured is beyond both our knowledge and the scope of this study. Therefore, we handled our multivariate models in the following way. We reduced each initial model stepwise by excluding the confounding variable with the highest p-value in each step until only $p<0.1$ predictors remained; we inspected the models in each step and never excluded our predictor of interest, i.e. urbanization. The aim of this process was to increase the accuracy of effect size estimates for urbanization; effect sizes in full models are usually inaccurate because there are many noise terms (Hegyi & Garamszegi 2011). Note that our final models yielded qualitatively the same conclusions as the full models (i.e. when no stepwise selection was done). We present effect size estimates (Cohen's *d*) with 95% confidence intervals for the variables retained in the final models, mean ± SE for bivariate comparisons and two-tailed p-values throughout the paper. All statistical analyses were performed in the R computing environment (R 2.11.0; R Development Core Team 2010), using the 'nlme' package.

3. RESULTS

3.1. Population trends

The TRIM analysis indicated a significant, moderate decline of the house sparrow in Hungary ($b \pm SE = -0.022 \pm 0.008$, $p<0.01$) during the studied period (Fig. IV.2). This country-wide decline was paralleled by a decrease in nest box occupancy and total number of fledglings produced per year at our suburban study site in 2005-2010, over 6 years of the studied period (Fig. IV.2).

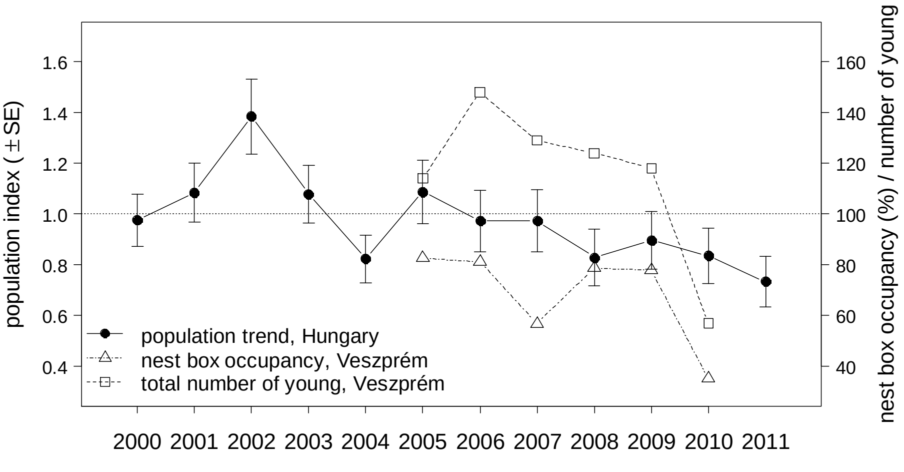

Fig. IV.2. Temporal trends in house sparrow population size in Hungary. Population index refers to the difference in population size between the given year and the starting year of the monitoring scheme (1999; marked by a dotted line). Nest box occupancy and total number of young are shown for the suburban site of the field study of reproduction.

3.2. Reproduction, nestling growth and chick feeding in the field

Median clutch size was 5 eggs in both habitats and both years (Table IV.2). Hatching success was not different between rural and suburban nests (Table IV.2); median number of hatchlings was 4 in both habitats and both years. In contrast, the number of nestlings before fledging was significantly higher in rural than in suburban nests (Table IV.2, Fig. IV.3), and broods in both habitats were larger in 2009 than in 2010 (habitat × year interaction: p=0.671; Table IV.2, Fig. IV.3). Thereby fledging success was higher in rural than in suburban nests and in 2009 than in 2010 (habitat × year interaction: p=0.146; Table IV.2). The number of broods raised successively in a given nest was similar in both habitats in both years (Table IV.2). Suburban nestlings had significantly smaller body size at the same pre-fledging age than rural nestlings (Table IV.2, Fig. IV.5): the former had on average ca. 4 g less weight, 0.7 mm shorter tarsi and 2 mm shorter wings than the latter. The difference between suburban and rural habitats was similar in the two years for body mass and wing length, but it tended to be greater for tarsus length in 2010 (Table IV.2, Fig. IV.5).

Table IV. 2. Generalized linear mixed-effects models of breeding success and nestling growth in field nests (habitat: suburban compared to rural; year: 2010 compared to 2009).

	b **± SE**	**p**	**Cohen's *d* (CI)**
Clutch size (196 broods at 115 nest sites)			
intercept	1.56 ± 0.03	--	--
year	-0.017 ± 0.034	0.609	-0.10 (-0.47; 0.27)
habitat	0.006 ± 0.034	0.865	0.03 (-0.34; 0.41)
Hatching success (173 broods at 108 nest sites)			
intercept	-0.32 ± 0.06	--	--
year	0.061 ± 0.060	0.313	0.16 (-0.15; 0.46)
habitat	0.075 ± 0.060	0.219	0.19 (-0.11; 0.49)
Pre-fledging brood size (146 broods at 93 nest sites)			
intercept	1.31 ± 0.09	--	--
year	-0.24 ± 0.104	0.024	-0.48 (-0.92; -0.07)
habitat	-0.352 ± 0.106	0.001	-0.7 (-1.15; -0.27)
Fledging success (146 broods at 93 nest sites)			
intercept	-0.08 ± 0.09	--	--
year	-0.208 ± 0.098	0.036	-0.45 (-0.89; -0.03)
habitat	-0.3 ± 0.099	0.003	-0.64 (-1.09; -0.22)
Number of broods per nest site (109 nest sites)			
intercept	0.43 ± 0.09	--	--
year	-0.078 ± 0.093	0.406	-0.16 (-0.55; 0.22)
habitat	0.043 ± 0.097	0.657	0.09 (-0.30; 0.47)
Nestling body mass (455 nestlings from 137 broods at 98 nest sites)			
intercept	25.03 ± 0.60	--	--
year	-1.649 ± 0.665	0.015	-0.51 (-0.94; -0.1)
habitat	-4.381 ± 0.691	<0.001	-1.3 (-1.81; -0.84)
Nestling tarsus length (453 nestlings from 136 broods at 97 nest sites)			
intercept	14.4 3± 0.93	--	--
year	0.598 ± 0.276	0.033	0.46 (0.05; 0.88)
date	0.009 ± 0.003	0.003	0.62 (0.21; 1.06)
brood size	0.185 ± 0.077	0.021	0.51 (0.1; 0.94)
age	0.22 ± 0.075	0.004	0.62 (0.2; 1.06)
habitat	-0.709 ± 0.326	0.032	-0.46 (-0.89; -0.05)
habitat × year	-0.955 ± 0.482	0.051	-0.42 (-0.84; -0.01)
Nestling wing length (436 nestlings from 133 broods at 97 nest sites)			
intercept	11.00 ± 3.61	--	--
year	-1.403 ± 0.871	0.111	-0.33 (-0.75; 0.07)
age	3.289 ± 0.325	<0.001	2.1 (1.56; 2.74)
habitat	-2.249 ± 0.941	0.019	-0.5 (-0.93; -0.09)

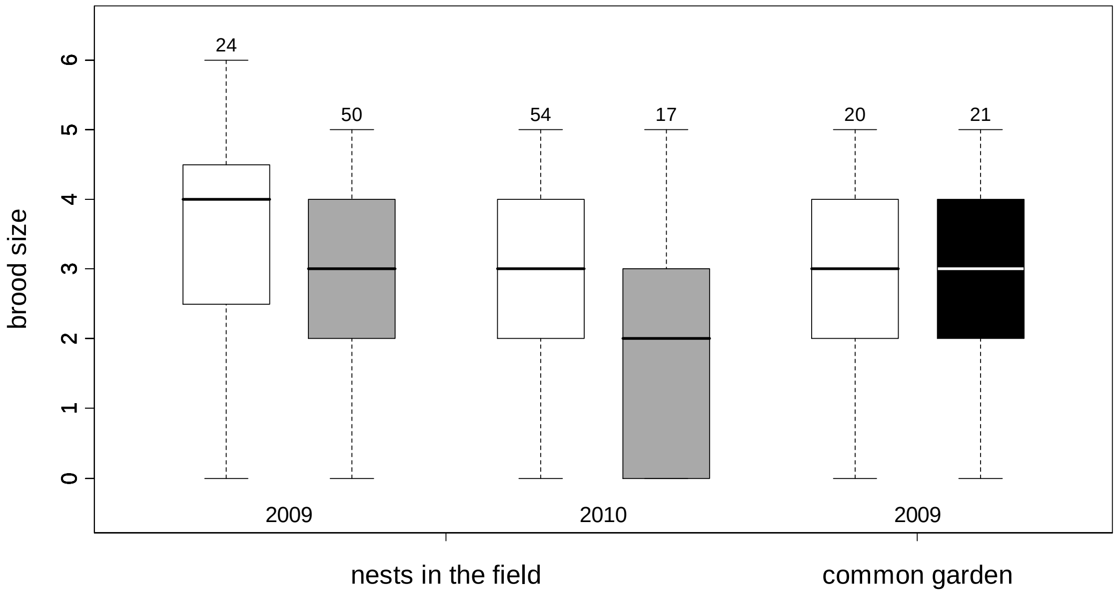

Fig. IV.3. Brood size before fledging in rural (white) and suburban (grey) nests in the field, and by pairs from rural (white) and urban (black) habitats in the common garden experiment in 2009. Number of nests is shown above each boxplot. Medians, interquartile ranges and data ranges are shown by the middle thick lines, the boxes, and the whiskers, respectively.

The chick-feeding rates (i.e. number of feeding / nestling / observation) was similar in rural (0.91 ± 0.06 SE) and suburban nests (0.77 ± 0.12 SE; Table IV. 3). In contrast, rural parents delivered more 'e-prey' to their chicks: the exp-transformed parameter estimate of Table IV. 3 indicates that there is ca. 77% less chance for e-prey deliveries in suburban compared to the rural habitat. Furthermore, date (i.e. number of days passed from April 1st) and greater brood size also predicted increasing 'e-prey' rate (i.e. large food items / all recognized food items; Table IV.3), although we found no significant difference in nestling numbers of the surveyed rural (4.07 ± 0.13 SE) and suburban (4.15 ± 0.16 SE) nests (Welch test t_{92} = -0.35, P = 0.725). 'E-prey' was delivered typically < 1 time during a food delivery survey (0.75 ± 0.08 in rural, 0.3 ± 0.07 in suburban broods).

Table IV. 3. Final generalized linear mixed-effects model of 'e-prey' rate in field nests (habitat: suburban compared to rural). We considered every food item as an 'e-prey' when it was larger than the parent's bill (>2 cm).

	b **± SE**	**p**	**Cohen's *d* (CI)**
Parents' feeding rate (71 broods, 193 observations)			
intercept	626.48 ± 129.26	--	--
date	-0. 004 ± 0.002	0.04	-0.3 (-0.59;-0.02)
year	-0.31 ± 0.06	<0.001	-0.7 (-1.01; -0.41)
habitat	-0.12 ± 0.12	0.322	-0.15 (-0.43; 0.14)
number of nestlings	-0.26 ± 0.04	<0.001	-0.94 (-1.27; -0.64)
"E-prey" rate (61 broods, 137 observations)			
intercept	-3.01 ± 0.84	--	--
date	0.019 ± 0.005	0.002	0.56 (0.23; 0.93)
habitat	-1.09 ± 0.414	0.013	-0.45 (-0.81; -0,11)
number of nestlings	0.307 ± 0.149	0.047	0.35 (0.01; 0.70)

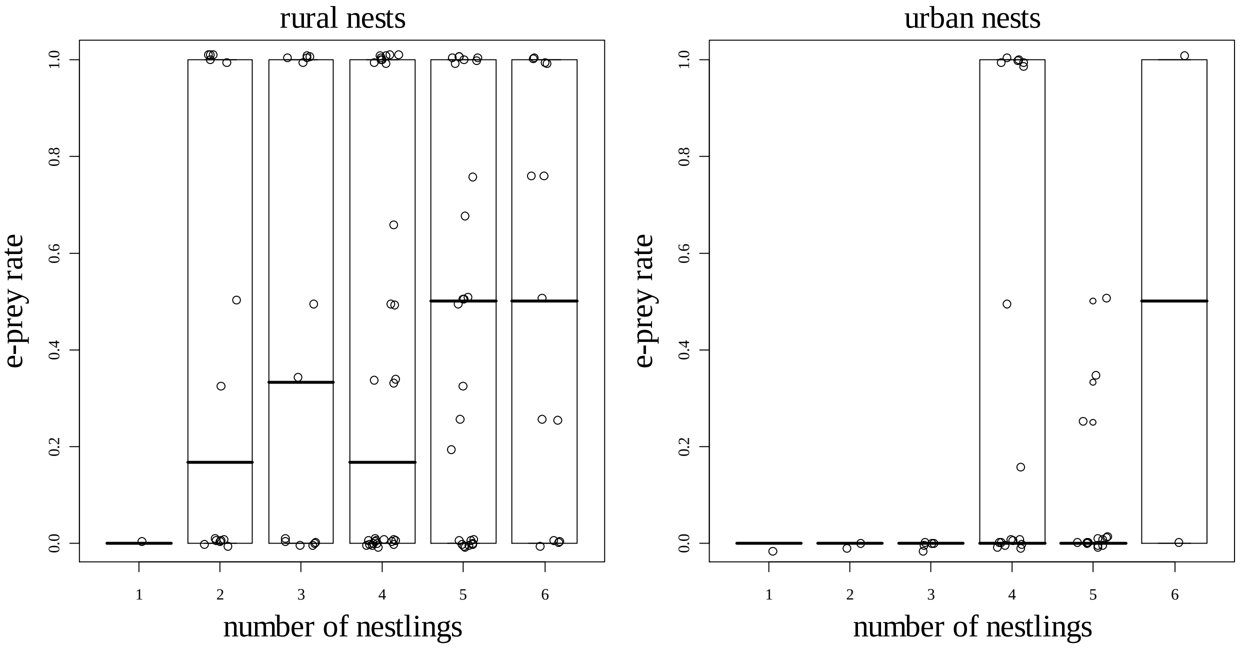

Fig. IV.4. Relationship of nestling number and the delivered e-prey rate in the 47 rural (left) and 17 suburban (right) nests.

3.3. Manipulations of the rearing environment

(a) Common garden experiment

In the aviaries in 2008, nestlings of urban pairs had similar body mass prior to fledging (18.14 ± 3.77 g, n=10 nestlings by n=2 pairs) as nestlings of rural pairs (19.56 ± 3.31 g, n=16 nestlings by n=5 pairs; LME: t_5=0.45, p=0.674). In 2009, median clutch size was 4 eggs for both rural and urban pairs (Table IV.4); 18 out of 38 rural and 9 out of 30 urban nesting attempts failed to hatch nestlings. The apparently higher rate of unsuccessful nesting attempts in rural birds was mainly due to one pair who laid 7 clutches that all failed to hatch. Among the nests that hatched at least one nestling, hatching success was not different between rural and urban pairs (Table IV.4); median number of hatchlings was 3.5 for rural pairs and 3 for urban pairs. The median number of nestlings before fledging was 3 for both rural and urban pairs (Table IV.4, Fig. IV.3), thus they had similar fledging success (Table IV.4). Nestlings' body mass, tarsus length, and wing length did not differ significantly between rural and urban pairs (Table IV.4, Fig. IV.5). Among the 23 young that survived to adulthood (i.e. September), birds of urban and rural origin had similar body mass (27.02 ± 2.69 g *versus* 27.22 ± 2.25 g; LME: t_8=0.54, p=0.605) in both years (habitat × year interaction: p=0.164). Urban and rural parents fed their nestlings at similar frequency (Table IV.4).

Captive birds' brood size was similar to (Fig. IV.3) and nestling body mass was larger than (Fig. IV.5) those observed in the 'neighboring' free-living suburban sparrows in the same year (t_{246}=7.94, p<0.001). The proportion of hatched nestlings that survived until pre-fledging age per brood (0.94 ± 0.03) was also significantly higher than the survival rate we observed in suburban broods in the field (0.66 ± 0.05; t_{85}=4.09, p<0.001).

Table IV. 4. Generalized linear mixed-effects models of breeding success and nestling growth in the common garden experiment in 2009 (habitat refers to the origin of captive birds, i.e. urban compared to rural).

	b ± SE	p	Cohen's *d* (CI)
Clutch size[1]			
habitat	-0.098 ± 0.096	0.322	-0.47 (-1.5; 0.46)
Hatching success[2]			
date	-0.003 ± 0.002	0.044	-1.08 (-2.36; -0.05)
habitat	-0.050 ± 0.138	0.721	-0.18 (-1.23; 0.82)
Pre-fledging brood size[3]			
date	-0.006 ± 0.003	0.041	-1.09 (-2.38; -0.06)
habitat	0.070 ± 0.171	0.686	0.21 (-0.79; 1.26)
Fledging success[4]			
habitat	0.216 ± 0.132	0.122	0.79 (-0.21; 1.98)
Nestling body mass[5]			
habitat	0.368 ± 0.872	0.678	0.20 (-0.8; 1.25)
Nestling tarsus length[6]			
age	0.350 ± 0.176	0.064	1.00 (-0.02; 2.26)
habitat	0.254 ± 0.275	0.368	0.46 (-0.53; 1.56)
Nestling wing length[7]			
age	4.973 ± 0.843	<0.001	2.95 (1.49; 5.13)
habitat	1.041 ± 1.110	0.362	0.47 (-0.52; 1.58)
Parents' feeding rate[8]			
nestlings' age	0.145 ± 0.041	<0.001	0.42 (0.18; 0.65)
parent's sex	0.163 ± 0.560	0.771	0.03 (-0.20; 0.26)
sex × age	-0.231 ± 0.057	<0.001	-0.47 (-0.71; -0.24)
date	0.008 ± 0.004	0.069	0.22 (-0.02; 0.45)
habitat	0.112 ± 0.360	0.759	0.04 (-0.19; 0.27)

[1] Intercept: 1.40±0.06; n=68 broods by 21 pairs

[2] Intercept: -0.03±0.18; n=41 broods by 19 pairs

[3] Intercept: 1.50±0.27; n=41 broods by 19 pairs

[4] Intercept: -0.25±0.09; n=41 broods by 19 pairs

[5] Intercept: 24.39±0.64; n=112 nestlings from 36 broods by 19 pairs

[6] Intercept: 14.80±1.65; n=111 nestlings from 36 broods by 19 pairs

[7] Intercept: 30.48±1.82; n=111 nestlings from 36 broods by 19 pairs

[8] Intercept: 0.86±0.55; n=294 observations for 37 broods by 19 pairs

(b) Cross-fostering experiment

Irrespective of their origin (i.e. hatching environment), nestlings in rural nests tended to grow larger than nestlings developing in suburban nests; this trend was most pronounced for tarsus length (Fig. IV.5). On the other hand, nestlings that hatched in different habitats but were raised in the same habitat showed less consistent tendencies in body size differences, i.e. rural-hatched nestlings had somewhat smaller body mass and wing length but similar or slightly longer tarsi than suburban-hatched nestlings when reared in the same environment (Fig. IV.5).

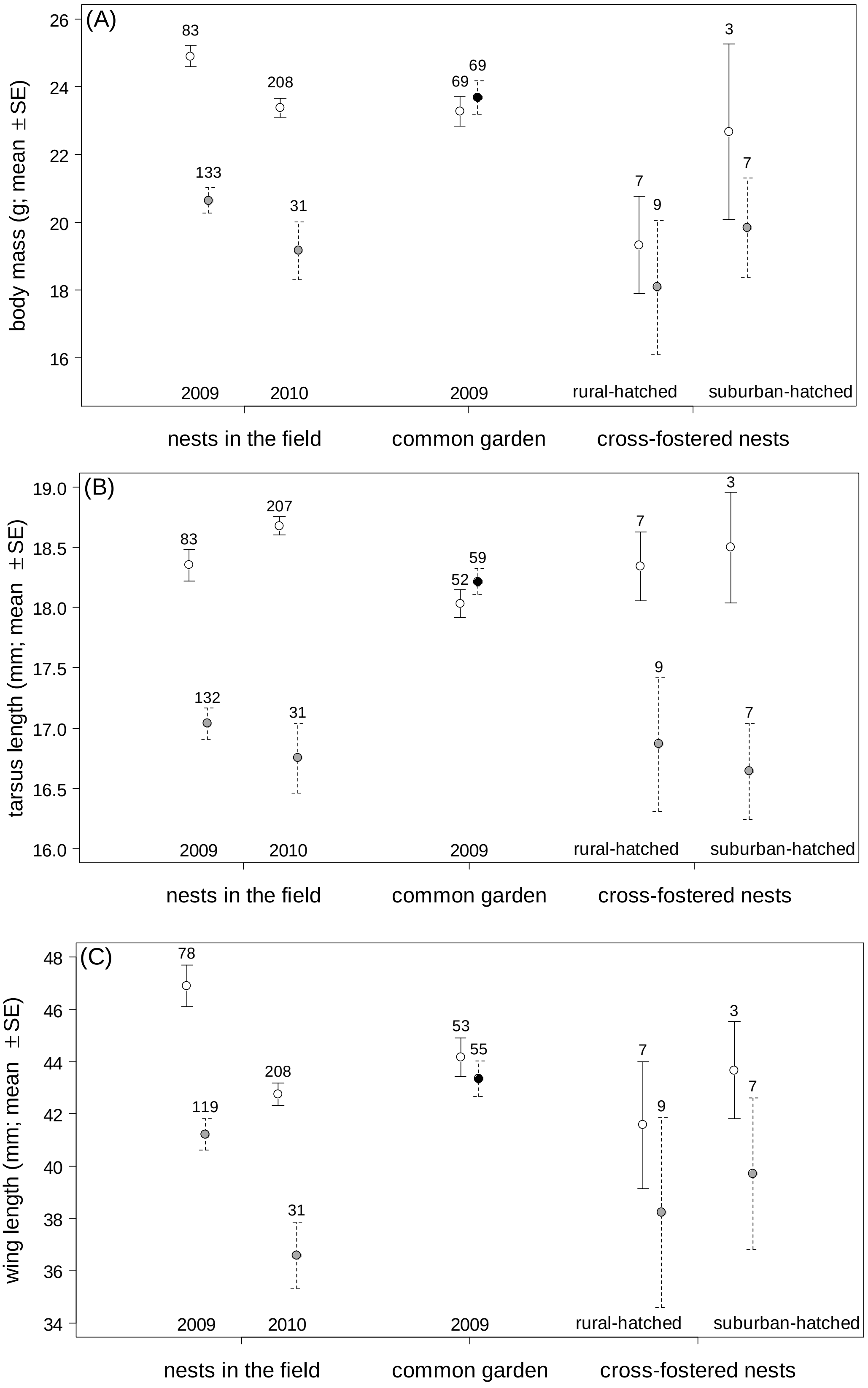

Fig. IV.5. Nestling growth in rural (white) and suburban (grey) nests in the field, and in nests of rural (white) and urban (black) pairs in the common garden experiment. The number of nestlings is shown above each error bar.

4. DISCUSSION

This study investigated several aspects of breeding performance of rural and suburban house sparrows, and has provided four key results. First, the national monitoring data indicate a moderate decline in the Hungarian house sparrow population for the last decade, that is paralleled by the decreasing nest box occupancy and fledgling number in our suburban study site. Second, we found that the growth and survival of nestlings was reduced in suburban nests, demonstrating that house sparrows may have similar difficulties with breeding in urbanized habitats in our moderately declining central-European population as in the rapidly declining British population. Third, our direct observations of parents' food deliveries revealed that suburban sparrows brought less 'e-prey' to their nestlings than rural parents, thus nestlings received less and/or lower quality food in more urbanized areas. Finally, we obtained two independent lines of experimental evidence that the rearing environment of nestlings plays a key role in the observed habitat differences in house sparrows' breeding success. We provide a detailed discussion of these results below.

The limited information that is available on the status of house sparrow populations in central European countries indicates a slight to moderate decline in this region (Kelcey & Rheinwald 2005; Reif *et al.* 2006). Our data on the Hungarian population revealed a similar trend, supporting the anecdotes we often hear about 'disappearing' sparrows. Despite any difference between Hungary and Britain in both the status of house sparrow populations and the structure of urban and rural habitats, our comparative results on the sparrows' reproductive performance show striking similarity to those of Peach *et al.* (2008). In both studies, suburban and rural birds had similar clutch sizes and number of broods (at the same nest site) but the former raised consistently less nestlings per nesting attempt than the latter due to reduced survival between hatching and fledging. Also, suburban fledglings were smaller than rural fledglings in both studies, suggesting that the former had reduced chances of post-fledging survival (Schwagmeyer & Mock 2008) and, even if they reach adulthood, they cannot make up for their arrears in body size (Liker *et al.* 2008). Interestingly, the difference between habitats was approximately twice as large in our study as those reported in the Leicester study (Peach *et al.* 2008) for both brood size (ca. 1 versus 0.4 nestlings per nest) and nestlings' body size (4.38 g versus 1.85 g). Furthermore, our rural birds produced more and larger offspring than their suburban counterparts not only in the 'good year' (as in the Leicester study) but also in the 'bad year'. Whereas Peach *et al.* (2008) found that weather conditions had stronger effect on the sparrows' breeding success than habitat characteristics (although nitrogen-dioxide levels seemed similarly important as temperature), differences between rural and suburban nests in our study were at least as large as, or even larger (see Fig. IV.3) than differences between the two years with markedly different weather. Altogether, these results suggest that the poor productivity of suburban sparrows in Britain and Hungary may represent a general trend, and even the less steeply declining populations may be vulnerable to any further negative effects of habitat urbanization (such as increased predation risk from urbanizing sparrowhawks, Bell *et al.* 2010) since they are already suffering decreases in reproductive success in the suburbs.

Some of our results are in line with the general patterns reported for urban passerines, as they are usually characterized by lower nestling body mass and fewer fledglings per breeding attempt (e.g. see the meta-analysis of Chamberlain *et al.* 2009a). Contrarily to the findings of this meta-analysis, however, our suburban and rural nests did not differ markedly either in average clutch size or in hatching success, and we did not find differences in the estimated number of subsequent broods per pair. Earlier egg-laying date in cities is also a general phenomenon (assumed to be a response to the more predictable food sources and milder microclimate; e.g. Chamberlain *et al.* 2009a; Evans 2010), but we could not investigate this aspect of breeding biology between our populations due to the lack of sufficient amount of standardized data on laying dates.

The reduced body mass, size and the lower number of fledged chicks in our suburban population might be due to the elevated anthropogenic noise level that characterizes e.g. urbanized habitats. In their study Schroeder *et al.* (2012) found that sparrow females of noisy territories delivered less food and reared chicks of lower number and reduced quality compared to those nesting in less noisy areas. Although we suppose that our suburban study site has indeed higher noise levels (we do not have any data on it), none of our suburban nest-boxes was in such extreme noisy environment than nests in the Schroeder-study, and we did not find any significant differences in habitat-related parental food delivery rates as it would be presumed by the results of the above study.

It is known that availability of nestling food is one of the most crucial factors limiting birds' reproductive success (also called as the 'bottleneck' of successful parental care) with higher food availability generally resulting in better chick development and survival. The length of the period between sparrows' hatching and fledging is short (c.a. 2 weeks in our region) and characterised by continuous and intensive development of nestlings. Also, tarsus length nearly reaches its maximum at about 10 days of age (Anderson 2006; personal observations); hence, the early nutritional conditions strongly affect both chicks' survival and skeletal development. While it is generally accepted that urban areas have higher densities of more predictable food sources (e.g. Shochat 2004), a great proportion of these are anthropogenic originated, lower quality food. Inadequate nestling diet is often assumed to be a major cause for the low productivity and thereby the declines observed in urbanized sparrows (De Laet & Summers-Smith 2007; Shaw *et al*. 2008; Peach *et al*. 2008; Chamberlain *et al.* 2009a). Although our results do not show any habitat-related differences in overall parental food delivery rates, it provides direct evidence for the hypothesis that suburban nestlings receive diet of lower quality and/or quantity as their parents delivered significantly fewer large prey items e.g. large caterpillars or orthopterans than those in rural habitats. These 'e-prey' seems to be the most valuable type of nestling food since its delivery rate strongly predicts fledging mass and recruitment (Schwagmeyer &Mock 2008). Furthermore, such differences in nestling diet is likely to affect not only nestling mortality, but the results of some experimental studies in the house sparrow (Anderson 2006) and song sparrow (*Melospiza melodia;* Searcy *et al.* 2004) suggest that such developmental fallbacks are carried over to adulthood.

Thus, from these results, we suggest that lower proportion of large food items and the reduced reproductive output of suburban pairs may reflect the shortage of key arthropod prey for nestlings in urbanized areas. For example, the increased loads of pollutants in urban habitats may also affect sparrows adversely in both directly (physiological and biochemical responses) or indirectly (e.g. effects on food base). In urban areas enhanced levels of bioaccumulation of such contaminants (e.g. heavy metals) has already been demonstrated in sparrows (Kekkonen 2011; Bichet 2013), their detrimental, synergistic effects on birds' physiology is documented by several studies (e.g. Outridge & Scheuhammer 1993; Eeva & Lehikoinen 1996) and it also known that young individuals are more sensitive in general (Scheuhammer 1987), suffering e.g. from higher mortality, reduced body mass and condition (e.g. Janssens *et al.* 2003). Additionally, as an indirect effect it also plausible that these contaminants may reduce the available invertebrate food in urban areas which is essential for proper chick development. This theory has been underscored by Peach *et al.* (2008) who reported some correlative findings between traffic-related air pollution and poor reproduction success in house sparrows. As a consequence of low arthropod density, parents may be forced to compensate by collecting whatever they can, e.g. seeds, bread crumbs, subsidized food for pets and other household scraps which do not contain the essential nutrients that are beneficial for chicks' growth (e.g. Vincent 2005; Anderson 2006). In their study Schwagmeyer & Mock (2008) made an attempt to translate invertebrate food size into food value and estimated that a single large prey item's (c.a. >2 cm) dry weight is 30-40 times greater, thus it is significantly more valuable than a small one (< 0.6 cm). It is not yet known, however, whether 'e-prey' is superior merely due to the disproportionately larger quantity of nutrients it provides (Schwagmeyer & Mock 2008) or because it represents specific taxa of particular nutritional value (e.g. spiders contain high levels of taurine, Ramsay & Houston 2003). In either case, urbanization is likely to reduce diet quality for sparrow nestlings because they are primarily fed by beetles, caterpillars, flies, spiders and aphids (Anderson 2006). With the exception of aphids, these taxa tend to show reduced abundance and/or diversity with increasing urbanization (Shochat *et al.* 2004; McIntyre & Rango 2009; Niemelä & Kotze 2009; Raupp *et al.* 2010), whereas arthropods un- or positively affected by urbanization are typically smaller sized (such as aphids) or unavailable for sparrows (e.g. leaf-mining moths or gall-forming taxa; Raupp *et al*. 2010). Furthermore, the size of individual arthropods within taxa is also reduced in urbanized and polluted environments (Niemelä & Kotze 2009; Zvereva & Kozlov 2010), which may further decrease the availability of 'e-prey'. Peach *et al.* (2008) found that nestling survival was positively correlated with aphid abundance which might indicate that the lack of 'e-prey' could be (at least in part) compensated for by smaller prey that is available in urban environments. However, the authors suggested that their finding reflects a correlation between the abundance of aphids and other invertebrates rather than any dependence of sparrow nestlings on aphids.

Additionally, the importance of nestling diet is further highlighted by our common garden experiment, which showed that urban and rural sparrows perform equally well in every aspect of reproduction if they live in the same environment with ample supplies of arthropod prey. Birds captured at urban sites showed no sign of reduced fertility or parental quality as an eventual consequence of their previous urban life. Thus, although adult sparrows from more urbanized habitats have smaller body mass (Liker *et al*. 2008; Bókony *et al*. 2010, ***Chapter III***), their reproductive capacity does not seem to be inferior to that of rural sparrows. Furthermore, the captive birds' nestlings grew larger than those of the free-living suburban birds, reaching similar size as the chicks of the free-living rural birds (see Fig. IV.3). Because the captive birds experienced the same weather conditions and pollution levels as the free-living suburban birds but had *ad libitum* access to nestling food, we might infer that the latter may be the most important determinant of breeding success for sparrows while weather and pollution seems to affect them *via* their effects on the availability of arthropods rather than directly. However, our rural and suburban study sites may have also differed in predation pressure, which may affect chick's growth via influencing their parents' behavior. Higher perceived predation pressure on adults may either limit their food gathering behaviour, or also, parents may decicide to rear smaller fledgelings as smaller size may be adaptive when predation risk is elevated.

The trends revealed by our cross-fostering experiment provide additional support for the importance of environmental conditions during nestling development. Despite the limited sample size that was forced upon us by the harsh weather conditions of 2010 which resulted in the birds' low willingness to breed and high nest failure rates, the direction of every difference observed between rural and suburban birds was in accordance with our predictions. Specifically, irrespective of their origin, nestlings raised in rural nests tended to grow larger than those raised in suburban nests, whereas birth habitat had no consistent effect on nestling growth, i.e. rural-hatched nestlings reached similar (or even slightly smaller) size than suburban-hatched nestlings under similar rearing conditions. Coupled with the results of the common garden experiment, these findings strengthen the evidence for causality in the relationship between urbanization and decreased breeding success in house sparrows that has been suggested by correlative studies in both Britain (Peach *et al.* 2008) and Hungary (this study). As sparrow nestlings cannot be sexed by appearance, we cannot exclude the possibility that sexual dimorphism in nestlings' body size might have influenced our results. However, the effect of sex on nestling morphology is small compared to the effect of habitat we have found and it is not consistent for different body parts (Kinnard & Westneat 2009) whereas in our study all morphological measures differed consistently between suburban and rural birds.

Finally, our results also provide some information on the effects of urbanization on adult sparrows in the breeding season. Both in the field and in the common garden experiment, adult birds of differently urbanized habitats did not differ in clutch size, hatching success, and the number of broods raised successively per nest site which may be indicative of the seasonal breeding success per pair. These findings suggest that adults are unlikely to be in inferior body condition or poor health at more urbanized sites, supporting the conclusion of our previous studies on sparrows' competitive performance (Bókony *et al.* 2010) and body condition indices (***Chapter III***). Although urban sparrows have consistently smaller body mass than rural conspecifics (Liker *et al.* 2008; Bókony *et al.* 2010, 2012), this seems to be a life-long consequence of impaired nestling growth resulting in reduced body size but apparently similar individual quality.

Taken together, our results consistently support that, for house sparrows, the primary 'victims' of habitat urbanization are the nestlings, suffering increased mortality and reduced growth due to the lack of adequate food such as 'e-prey'. Similarly to our findings, the nestlings of European starlings (*Sturnus vulgaris*) and American crows (*Corvus brachyrhynchos*) were also found to reach inferior body size in more urbanized habitats compared to those of rural areas due to the insufficient nestling diet (Mennenchez & Clergeau 2006; Heiss *et al.* 2009). The major implication of our study for conservation is that these negative effects may well be at work not only in conspicuously declining house sparrow populations but also in those that appear steady, or even in those that are not being considered from any conservational aspect.

CHAPTER V

Response to predation risk in urban and rural house sparrows

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ABSTRACT

Habitat urbanization may change the density of predators, and it is often assumed that such changes lead to altered predation risk for urban populations of their prey. Although it is difficult to study predation hazard directly, behavior responses of prey species may be informative in inferring such habitat differences. In this study, we compared the risk-taking behavior of urban and rural house sparrows after simulated attacks by two of their important predators (sparrowhawk and domestic cat). The birds were startled by moving dummies of these predators and respective control objects, and their risk taking was estimated as their latency to feed after the startle. We found that sparrows responded more strongly (had longer post-startle feeding latencies) to sparrowhawk attacks than to the control object, and their responses differed between the habitats. First, risk taking of urban birds strongly decreased with age (older birds had longer latencies than young birds), while there was no such age difference in rural birds. Second, young urban birds responded less strongly, while older urban birds responded more strongly to the sparrowhawk than the same age groupsof rural birds, respectively. We did not succeed in evoking antipredatory response by simulated cat attacks, because birds responded similarly to the dummy and the control object. Our results support that predation risk, posed at least by avian predators, is different in urban and rural habitats of house sparrows. The increased wariness of older, hence presumably more experienced, urban birds implies that sparrows may be more exposed to predation in cities.

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1. INTRODUCTION

Habitat urbanization alters several ecological factors that shape the composition and structure of animal communities (Shochat *et al.* 2006). One of the most important ecological factors is predation pressure, which may have a strong effect on prey populations through lethal and non-lethal effects (Cresswell 2008). Despite its crucial role in population dynamics, it is controversial how predation risk for prey species changes along the urbanization gradient.

Predator densities often differ between differently urbanized sites. For example, domestic and feral predators (e.g. cats and dogs) may attain very high densities in urban areas (Sorace 2002). The abundance of native predators may be either reduced (Blair 2004) or increased, e.g. populations of some raptor species are currently increasing in cities (Chace & Walsh 2006; Rutz 2008). A recent large-scale study by Sorace & Gustin (2008) found that the abundance of predators changed in a complex manner with urbanization, e.g. differed between generalist vs. specialist species. In addition to these complexities, the density of predators in itself may not reflect the actual predation risk. For example, cats may act as predators of small birds and mammals (Lepczyk *et al.* 2003; Woods *et al.* 2003; Baker *et al.* 2008), but it is unclear whether they cause significant mortality as they may also rely on refuse or food provided by humans. Urban prey may attract rural raptors into the cities to hunt (Newton 1986), which may lead to greater predation than that suggested by the breeding densities of urban raptors. Finally, the mere presence of predators may be detrimental for prey populations via indirect effects such as starvation or suppressed breeding, which may be greater than the mortality effect (Cresswell 2008). Prey behavior and life history can reflect the risk of predation, thus providing a useful alternative approach to study habitat differences. To date, the results are similarly diverse as those inferred from predator densities. For example, field studies of birds' foraging behavior suggested lower predation risk in cities than desert areas (Shochat *et al.* 2004) and for more urbanized species (Tsurim *et al.* 2008). Chamberlain *et al.* (2009a) reported lower adult mortalities in urban populations of some passerines, although it is unclear whether this was the result of reduced predation. Similarly, the looseness of the rump feathers, which is thought to be an antipredatory adaptation, was found to be reduced in urban bird species compared to closely related rural species, implying that the former are less affected by density-dependent predation rates than the latter (Møller 2009). On the other hand, another study (Møller 2008) found that species with greater proportion of their population breeding in urban habitats are more susceptible to predation (i.e. occur more frequently in the diet of sparrowhawks than expected by chance), suggesting that increased abundance of urban birds (Møller 2009) makes them increasingly preferred as prey by the sparrowhawk (Møller 2008). House fiches (*Carpodacus mexicanus*) were also found to show increased levels of antipredatory behaviors in more urbanized habitats (Valcarcel & Fernández-Juricic 2009). In sum, the evidence of the relationship between habitat urbanization and pre-dation risk is ambiguous. Although lower predation pressure on adult birds in cities is a central assumption of some models of urban population dynamics (Shochat 2004; Anderies *et al.* 2007), the effect of urbanization on predation may well be species-specific in terms of both predator and prey species (Sorace & Gustin 2008).

In this study, we focus on predation risk experienced by urban and rural house sparrows. This species is common in many differently urbanized habitats and is an important avian prey of several predators such as feral cats and sparrowhawks (Sodhi & Oliphant 1993; Götmark & Post 1996; Gillies & Clout 2003; Baker *et al.* 2005). Whereas sparrow populations have been declining worldwide (Summers-Smith 2003; Shaw *et al.* 2008), several populations of their predators are increasing in urban habitats, including the sparrowhawk (Risch *et al.* 1996; Kelcey & Rheinwald 2005; Bérces 2007; Chamberlain *et al.* 2009b; Bell *et al.* 2010), other raptors (Sodhi & Oliphant 1992; Salvati *et al.* 1999; Morandini 2006; Rutz 2006), and the domestic cat (Woods *et al.* 2003; Beckerman *et al.* 2007). To test whether sparrows in differently urbanized habitats experience different levels of predation risk, we exposed wild-caught birds from several urban and rural populations to simulated predator attacks and measured their subsequent risk-taking behavior. The assumption behind our study was that the birds' responses to predator exposure reflect the level of predation risk they have adapted to in their original habitats. In accordance with this assumption, a meta-analysis showed that experience with predators amplifies the perception of risk, i.e. animals are generally more wary when they are more frequently exposed to predators (Stankowich & Blumstein 2005). For example, Fernández-Juricic *et al.* (2004) found that birds preferentially attacked by magpies (*Pica pica*) increased their scanning time in the presence of magpies relative to less often attacked species. Studies on three-spined sticklebacks (*Gasterosteus aculeatus*) and water fleas (*Daphnia magna*) experimentally demonstrated higher risk aversion in high-predation than in low-predation populations (De Meester 1996; Brydges *et al.* 2008). Therefore, if urban and rural sparrows experience consistently different levels of predation risk, we expect that the birds from the riskier habitat take less risk.

2. METHODS

2.1. Study subjects

In September 2009, we captured 58 house sparrows by mist-nets at five urban and five rural sites in Hungary (Table V.1). Urban sites were heavily built-up areas in centers of four cities (two sites 5.3 km apart from each other were used in Budapest), while rural sites were located on small farms in vegetated areas remote from city borders and also from each other. We chose study sites that represent independent local populations by being sufficiently far from each other to prevent significant exchange of birds between them (x ± SE distance between sites: 64.1 ± 6.4 km, range: 3.5–145.6 km). The house sparrow is a very sedentary bird: dispersal distances are typically 1–2 km (reviewed by Anderson 2006), and movements in the non-breeding season are usually <500 m (Liker *et al.* 2009; Vangestel *et al.* 2010).

Upon capture, we measured body mass (±0.1 g) and tarsus length (±0.1 mm) and ringed birds with a numbered aluminum ring and three color rings. By the development of the birds' plumage, we assigned them to two age categories: (1) young birds that did not have their complete adult plumage and (2) older birds with full adult plumage that were either adults older than 1 yr or juveniles fledged early in the breeding season of 2009. (We were not able to separate these two latter groups, but in any case they were older than the individuals categorized as young birds.)

Birds were transported to Veszprém and were housed in outdoor aviaries. These aviaries were ca. 3 m high and 3·4 m large, protected from rain and contained nest boxes and roosting trees. Birds had *ad libitum* access to food (millet, wheat, and sun-flower seeds) and water amended by multivitamin droplets. During the first 3 mo, birds were left undisturbed and kept in four mixed flocks of similar size in the aviaries, all containing birds from all capture sites to control for any eventual aviary effect. Before the risk-taking tests, ten birds died for unknown reasons; however, the rest of the birds remained in good health and condition. This rate of mortality was small compared to that observed in free-living house sparrows (Anderson 2006) and similar to other studies where sparrows were kept in aviaries (Liker & Bókony 2009; Bókony *et al.* 2010). Captures and housing were in accordance with the relevant Hungarian laws and were licensed by the Balaton Upland National Park (permission number: 9135-2⁄2004).

2.2. Test procedure

We tested each bird individually by exposing them to moving sparrowhawk and domestic cat dummies. These risk-taking tests were conducted in Jan.–Apr. 2010 during 1-week-long test periods. At the start of each test period, we captured two urban and two rural individuals from the aviary flocks; they were chosen randomly with the constraint that they were from different capture sites. Each bird participated in the experiment only once (i.e. was included in one 1-week test period). The identity of birds to be captured from the aviaries for each test period was determined before the beginning of the experiment; thus, the ease by which each individual could be captured had no effect on the order in which it participated in the experiment. During the whole study, a similar number of birds were tested from each capture site (rural capture sites: Vilmapuszta, Szentgál, Üllő-Dóramajor, Bánd, Salföld; urban capture sites: Várpalota, Veszprém, Budapest: Kőbánya-Kispest, Székesfehérvár, Budapest: VI. ker.; see details in Table III.1). After weighing (pre-test body mass), the birds were put into individual indoor cages (75 cm high, 80 x 45 cm large) containing a feeder, a water cup, three horizontal perches, a shelter box, and a small artificial bush. The wire grid bottom of the cages prevented the birds from accessing the seed spilled from the feeder. Birds were left undisturbed for the next 3 d with *ad libitum* food and water.

On the following 4 d, we tested one bird per day. Each bird participated in four consecutive tests, all conducted on the same day. Birds were tested in a room separated from the other birds. We alternated the testing of rural and urban birds, and the choice of the first bird of the week was randomized. Every individual's test consisted of two types of aerial (a predator and a control) and two types of ground (a predator and a control) treatments, and the sequence of treatments was randomized. At 3:00 p.m. before the test day, the actual test bird was placed in the test cage that was identical to the housing cages and contained the same food. The bird was left alone to feed until 4:00 p.m., and then the feeder lid was closed, so an overnight fasting preceded the next day's tests. At 8:00 a.m. on the test day, the lid of the feeder cup was opened remotely (from another room) by pulling a string. When the bird first pecked from the feeder, we startled it instantly by one of the treatment objects. If an individual did not peck from the feeder at all, the startle occurred 15 min after the feeder's opening. After the startle, the bird had up to 30 min to approach the feeder again and then had 10 min for feeding. After this period (or after 30 min if the bird did not resume feeding after the startle), the lid of the feeder was closed remotely, and a 60-min-long fasting period followed to ensure the birds' motivation for feeding in the next test. After the four consecutive tests, the bird was free to feed until 3:00 p.m.; then, we put it back to its former housing cage and moved the next bird to the test cage. After the 4th test of the 4th individual (i.e. at the end of the week), all four birds were weighed again (post-test body mass) and released back to the aviaries.

The aerial predator was a taxidermy-mounted sparrowhawk with body and wings in gliding posture and was moved on a wire ca. 1 m above the test cage. The dummy was remotely pulled out from a hide at one end of the test room and, after passing above the cage, disappeared behind another hide at the other end. It was visible for ca. 3 s for the test birds. A light brown paper box, operated in the same way, was used as control (it had approx. the same size as the sparrowhawk: 15 cm high and 30 x 20 cm large). The ground predator was a taxidermy-mounted cat attached onto a rolling board (a wooden plate equipped with four wheels). It was pulled out from a hide, moved ca. 1.5 m in front of the test cage, and after it was visible for ca. 4 s, it disappeared behind another hide at the other side of the room. We used a light brown paper box of similar size as control (25 cm high and 45 · 30 cm large) that was moved on the same lane as the cat dummy. We used one dummy per predator type throughout the experiment, assuming that the birds' responses to these dummies are representative of responses to live predators in the wild.

During the tests, the test bird was observed through a one-way window and the feeder's lid and the test objects were operated by a single experimenter from an adjoining room. The bird's presence on the feeder was detected by a small infrared detector placed at the top of the test cage: each time (± 0.01 s) of arriving at and departing from the feeder was recorded on a computer. Additionally, the behavior of the test bird was recorded by a video camera. In the analyses, we used the infrared detector's recordings because these provided the most accurate measurements of the latencies, and the experimenter's observations and the video recordings were used to double-check these data.

2.3. Data analysis

To assess the birds' body condition prior to the tests, we quantified their body mass relative to their body size by calculating the scaled mass index as recommended by Peig and Green (2009, 2010). This index adjusts the mass of all individuals to that which they would have if they had the same body size, using the equation of the linear regression of log-mass on log-size estimated by type-2 (standardized major axis; SMA) regression. For the calculation of this equation, we used our earlier data on the body mass and tarsus length of 2345 adult house sparrows (our unpublished data). The regression slope was 1.71, and average tarsus length was 19 mm, thus we calculated the scaled mass index as pre-test body mass × (19 / tarsus length)$^{1.71}$ (Peig & Green, 2009, 2010).

Out of the 48 test birds, one died before its test day for unknown reasons and another one escaped, so we could finally use the data of 46 birds in total (30 young, 16 older). Using the infrared detector's data we calculated two variables for each individual in every test situation: (1) latency to first feeding, measured from the opening of the feeder ('pre-startle latency'); (2) latency to feed after the startle, measured from the appearance of the predator dummy or the control object ('startle latency'). Birds that did not feed before and/or after the startle stimulus were given maximum latencies (900 and/or 1800 sec, respectively). Out of the total of 92 aerial and 92 ground tests, pre-startle latencies were maximal in 18 aerial and 16 ground tests, whereas startle latencies were maximal in 17 aerial and 11 ground tests. Only one individual did not feed at all (i.e. had maximal latencies in each of its tests); additionally, 2 birds in the aerial tests and 2 birds in the ground tests did not feed both in the dummy and its control tests.

To compare the response (i.e. startle latencies) of urban and rural sparrows we used linear mixed-effects models that contained the following random factors: bird ID (i.e. the latencies of each bird in the control and predator tests were treated as non-independent measures), capture site, test group (i.e. the 4 birds tested in the same weekly test period) and the position of the housing cage. Separate models were used for the analysis of the aerial and the ground treatments to avoid interactions between more than three variables, because anti-predatory responses to different predators may show different interactions with variables such as habitat and age. Both models contained the following predictors: pre-startle latency, date, test day (order of the test birds within the week), and the scaled mass index as covariates, treatment type (control object or predator dummy), sex and age (young or older) as factors; and scaled mass index × habitat, sex × habitat, and habitat × age × treatment type interactions. Additionally, we tested the effects of treatment order by including the following three predictors. To test for habituation or sensitization during the day, we used a covariate giving the number of treatments the individual had received before the actual treatment (ranging 0-3; hereafter treatment order). Because experience in previous tests might affect the response to predatory attacks, we used two factors to encode whether the individual had received the respective control treatment (hereafter control-predator order) and the other predator treatment (hereafter cat-sparrowhawk order) before or after the predator treatment being analyzed.

We report the full model as recommended by Forstmeier and Schielzeth (2011). Then we reduced the full model by omitting the effect with the highest P-value step by step until only significant ($P < 0.05$) effects remained, but never omitted habitat and the random factor. We also report the final model obtained by this approach, as recommended by Hegyi and Garamszegi (2011). We favored this model selection technique over the information-theoretic approach because it was suggested that the latter reduces the accuracy of effect size estimation for experiments designed to test the effect of one or two treatments (Richards *et al.* 2011), and our aim was to infer whether or not habitat has a considerable effect while controlling for confounding variables, rather than to compare the strength of evidence for each predictor. To check the robustness of our results, we re-ran all the analyses by omitting those cases in which the birds had maximal startle latency values (n=17 tests in aerial and n=11 tests in ground tests).

We also tested whether urban and rural birds differed in body mass change during the experiment because this may reflect their sensitivity to stress caused by the experimental conditions. For each bird we calculated the difference between pre-test mass (i.e. when the bird was captured from the aviary) and post-test mass (i.e. when the bird was released back into the aviary). The full linear mixed-effects model for body mass change contained habitat, sex, age and test day as fixed factors, date as covariate, the sex × habitat, age × habitat and date × habitat interactions, and capture site, test group, and housing cage as random factors. Stepwise model selection was performed as described above but we never omitted the age × habitat interaction.

Finally, to assess the potential effect of habitat or age differences in neophobia (i.e. fear of novelty) on the birds' responses in the test situations, we also analyzed (1) the birds' first pre-startle latencies, i.e. those after the first opening of the feeder (note that feeder lids were always open in the housing cages), and (2) the birds' startle latencies in the ground control treatment by using linear mixed-effects models. Responses in these novel situations, i.e. the first encounter with the feeder lid opening up and the paper box moving on the ground, may reflect the birds' neophobia. The full models contained habitat, sex, age, pre-test body mass, date, test day, and habitat × age, habitat × mass and habitat × sex interactions; and additionally, treatment order and pre-startle latency in the analysis of startle latency in the ground control treatment. Capture site, test group, and housing cage were included as random factors. We performed stepwise model selection as described above but never omitted the habitat × age interaction. Since the full model yielded qualitatively the same results as the final stepwise model in each case, for these additional analyses we only report the final models.

All statistical analyses were performed in the R computing environment (R 2.6.1; R Development Core Team 2010), using the nlme package. Statistical assumptions of linear models were checked and validated by diagnostic plots. Results are presented as mean ± SE, and all tests are two-tailed with a 5% significance level.

3. RESULTS

3.1. Birds' responses in test situations

Aerial treatments were successful in evoking behavioral response, as startle latencies were significantly higher than pre-startle latencies in both the sparrowhawk test (mean difference: 361.9 ± 79.3 sec; paired t-test: $t_{45} = 4.66$, $P < 0.001$; Fig. V.1) and in the aerial control test (mean difference: 180.2 ± 59.3 sec; paired t-test: $t_{45} = 4.13$, $P < 0.001$; Fig. V.1). In the cat test, birds had slightly but non-significantly longer latencies after than before the startle (mean difference: 102.9 ± 49.9 sec; paired t-test: $t_{45} = 1.75$, $P = 0.086$; Fig. V.1), but not in the ground control test (mean difference: 98.7 ± 71.2 sec; paired t-test: $t_{45} = 0.39$, $P = 0.696$; Fig. V.1).

The birds' startle latency was significantly longer in the sparrowhawk test than in the aerial control test (mean difference: 221.5 ± 102.3 sec; paired t-test: $t_{45} = 2.93$, $P = 0.005$; Fig. V.1); however, there was no significant difference in the startle latencies between the cat test and the ground control test (mean difference 75.9 ± 97.6 sec; paired t-test: $t_{45} = 0.71$, $P = 0.479$; Fig. V.1).

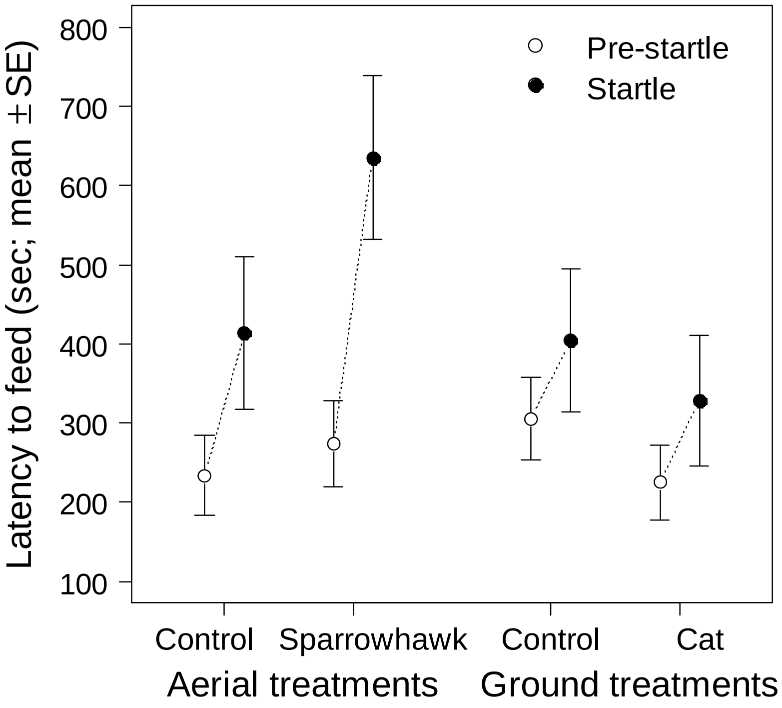

Fig. V.1 Pre-startle and startle latencies of birds in the four test situations (n=46).

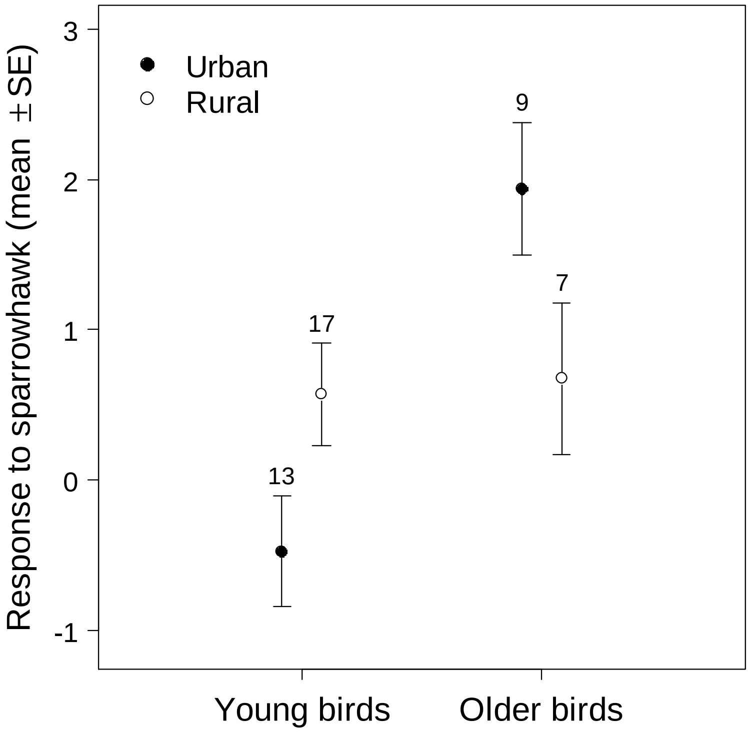

Fig. V.2 Response to the sparrowhawk dummy, expressed as the difference in residual startle latency between the raptor treatment and the aerial control treatment, in relation to habitat and birds' age. Residual startle latencies were calculated from a linear model containing pre-startle latency as predictor.

3.2. Differences between urban and rural birds

In the aerial treatments we found a strong habitat × age × treatment type interaction effect on the birds' startle latencies (Table V.1). Relative to the control treatment, risk taking after the sparrowhawk attack strongly decreased with age in urban birds (i.e. older birds had longer latencies than young birds), while there was no such difference in rural birds (Fig. V.2). Young urban birds responded less strongly, while older urban birds responded more strongly to the sparrowhawk attack than the same age groups of rural birds, respectively (Fig. V.2). Startle latency in the aerial tests was not significantly related to the scaled mass index and its interaction with habitat (Table V.1); using body mass instead of the scaled mass index yielded the same result (not shown). Startle latency did not vary consistently with test day and treatment order (Table V.1), suggesting that birds showed no habituation or sensitization overall during the experiment. However, the effect of control-predator order was significant (Table V.2): birds that had previous experience with the aerial control treatment showed weaker response to the sparrowhawk than those without such experience. Other predictors included in the initial model had no significant effect on the response to the sparrowhawk, except pre-startle latency (Table V.1). Omitting birds with maximal startle latencies did not change our results qualitatively in any analysis (habitat × age × treatment type interaction in the aerial tests: $P = 0.046$ in the full model and $P = 0.011$ in the final model, n = 42 birds).

In the ground treatments, startle latencies were not related significantly to any predictor or interaction considered; urban and rural birds did not differ in their response to the cat dummy (urban birds: mean 215.2 ± 84.1 sec; rural birds: mean 431.4 ± 136.3 sec; t-test: $t_{37.5} = 0.52$, $P = 0.604$) and the effect of the habitat × age × treatment type interaction was non-significant (linear mixed-effect model: $t_{46} = -0.25$, $P = 0.801$).

Urban birds had smaller pre-test body mass than rural birds, and this difference was similar in both age groups (linear model, habitat: $t_{42} = -2.41$, $P = 0.020$, age: $t_{42} = -0.89$, $P = 0.379$, habitat × age interaction: $t_{42} = -0.29$, $P = 0.777$; n=46 birds). The tarsus length of urban birds was also smaller (linear model, habitat: $t_{42} = -2.49$, $P = 0.017$, age: $t_{42} = 1.48$, $P = 0.147$, habitat × age interaction: $t_{42} = -0.95$, $P = 0.348$; n=46 birds), therefore the scaled mass index did not differ between urban and rural birds (linear model, habitat: $t_{42} = -0.13$, P = 0.899, age: $t_{42} = -1.98$, $P = 0.054$, habitat × age interaction: $t_{42} = 0.44$, $P = 0.664$). Furthermore, we found no significant habitat × age interaction in body mass loss during the experiment (Table V.2a). Our analyzes on the potential effect of neophobia on birds' responses showed that the habitat × age interaction was not significant for either the first pre-startle latency of the test day (Table V.2b) or the startle latency in the ground control treatment (Table V.2c).

Table V.1. (a) Full and **(b)** final linear mixed-effects model of birds' startle latencies in the aerial treatments (n=46).

	β ± SE	**t**	**P**	**Cohen's d (CI)**
(a)				
intercept	7.38 ± 3.50	2.11	0.038	0.80 (0.18; 1.49)
pre-startle latency	0.56 ± 0.08	7.17	< 0.001	2.71 (1.81; 3.85)
date	0.00 ± 0.01	0.29	0.772	0.11 (-0.49; 0.72)
test day	0.17 ± 0.14	1.25	0.216	0.47 (-0.13; 1.12)
habitat[1]	-5.79 ± 4.38	-1.32	0.191	-0.49 (-1.15; 0.10)
age[2]	0.29 ± 0.59	0.48	0.630	0.18 (-0.42; 0.79)
treatment type[3]	-0.52 ± 0.32	-1.60	0.113	-0.60 (-1.26; 0.00)
treatment order	0.01 ± 0.09	0.11	0.913	0.04 (-0.56; 0.65)
scaled body mass	-0.16 ± 0.11	-1.42	0.159	-0.54 (-1.19; 0.07)
control-predator order[4]	-0.80 ± 0.38	-2.14	0.036	-0.81 (-1.50; -0.19)
cat-sparrowhawk order[5]	-0.05 ± 0.35	-0.14	0.889	-0.05 (-0.66; 0.55)
sex[6]	0.41 ± 0.40	1.01	0.313	0.38 (-0.22; 1.02)
habitat × sex	-0.89 ± 0.58	-1.54	0.128	-0.58 (-1.24; 0.02)
habitat × scaled body mass	0.18 ± 0.15	1.18	0.240	0.45 (-0.16; 1.09)
habitat × age	1.79 ± 0.77	2.32	0.023	0.88 (0.25; 1.58)
habitat × treatment type	0.95 ± 0.49	1.91	0.060	0.72 (1.09; 1.39)
age × treatment type	-0.19 ± 0.61	-0.32	0.750	-0.12 (-0.73; 0.49)
habitat × age × treatment type	-2.29 ± 0.83	-2.77	0.007	-1.05 (-1.78; -0.41)
(b)				
intercept	3.43 ± 0.44	7.86	< 0.001	2.62 (1.73; 3.74)
pre-startle latency	0.56 ± 0.07	8.23	< 0.001	2.74 (1.84; 3.90)
habitat	-1.14 ± 0.44	-2.61	0.011	-0.87 (-1.57; -0.25)
age	0.49 ± 0.53	0.93	0.355	0.31 (-0.29; 0.94)
treatment type	-0.53 ± 0.32	-1.65	0.103	-0.55 (-1.20; 0.05)
control-predator order	-0.69 ± 0.28	-2.48	0.015	-0.83 (-1.52; -0.21)
habitat × age	1.66 ± 0.73	2.29	0.025	0.76 (0.15; 1.45)
habitat × treatment type	0.95 ± 0.49	1.95	0.055	0.66 (-0.04; 1.34)
age × treatment type	-0.19 ± 0.59	-0.33	0.743	-0.11 (0.73; 0.50)
habitat × age × treatment type	-2.28 ± 0.82	-2.80	0.006	-0.31 (-0.95; -0.30)

The models included bird ID, capture site, test group, and housing cage as random factors. Effect size estimates (Cohen's d) are given with 95% confidence intervals (CI). Non-significant terms included in the habitat × age × treatment type interaction were retained in the final model. Parameter estimates (β) express the effects of factors as differences between factor levels as follows: [1]rural – urban, [2]young – old, [3]predator dummy – control object, [4]control first – predator first, [5]cat first – sparrowhawk first, [6]female – male.

Table V.2. Final linear mixed-effects models of the birds' (a) body mass loss during the experiment, (b) first pre-startle latencies during the test day and (c) startle latencies in the ground control treatment (n=46).

	β ± SE	**t**	**P**	**Cohen's d (CI)**
(a)				
intercept	2.91 ± 0.49	5.91	< 0.001	1.85 (1.09; 2.77)
habitat	-0.46 ± 0.53	-0.85	0.398	-0.26 (-0.89; 0.34)
age	-1.08 ± 0.67	-1.62	0.112	-0.50 (-1.16; 0.10)
habitat × age	0.34 ± 0.78	0.43	0.665	0.13 (-0.48 0.76)
(b)				
intercept	6.19 ± 0.79	7.79	< 0.001	2.46 (1.61; 3.54)
habitat	0.43 ± 0.66	0.64	0.522	0.20 (-0.39; 0.82)
age	0.79 ± 0.89	0.89	0.380	0.28 (-0.32; 0.90)
sex	-1.28 ± 0.55	-2.34	0.024	-0.74 (-1.42; -0.13)
date	-0.03 ± 0.01	-2.16	0.036	-0.68 (-1.35; -0.07)
habitat × age	-1.11 ± 1.12	-0.99	0.325	-0.31 (-0.94; 0.29)
(c)				
intercept	1.63 ± 0.67	2.44	0.019	0.76 (0.14; 1.45)
pre-startle latency	0.67 ± 0.12	5.74	< 0.001	1.79 (1.06; 2.69)
habitat	0.26 ± 0.47	0.54	0.590	0.17 (-0.43; 0,79)
age	-0.36 ± 0.58	-0.63	0.534	-0.20 (-0.82; 0.40)
habitat × age	0.04 ± 0.80	0.05	0.958	0.02 (-0.60; 0.62)

The models included capture site, test group, and housing cage as random factors. Effect size estimates (Cohen's d) are given with 95% confidence intervals (CI). See Table V.1 for explanation of the parameter estimates.

4. DISCUSSION

In this study we investigated whether there are habitat-related differences in house sparrows' responses to the predation risk by two of their typical predators, the sparrowhawk and the domestic cat. We successfully simulated predation risk by sparrowhawk, because birds' startle latencies were higher than their pre-startle latencies, and startle latencies were higher following the sparrowhawk attack than following its control treatment. Our results showed that the risk taking of birds after the sparrowhawk attacks was related to both their age and original habitat in an interacting way. These findings support that sparrows are likely to experience different levels of predation risk in cities and rural sites, although the behavioral consequences are different in young and older birds. Because we included birds from several rural and urban localities, these results are likely to represent a general trend in our region and not the particular situation at a specific locality.

Two lines of evidence from this sparrowhawk test suggest that sparrows in cities may be exposed to greater predation risk than in rural habitats. First, response to the sparrowhawk attack increased strongly with age in the urban group, while no such increase was detected in rural birds. Such a difference is expected when predator attacks are more frequent in urban habitats, and gaining more experience with predators during an individual's life causes a larger increase in the birds' risk aversion (Stankowich & Blumstein 2005). Second, among older, hence presumably more experienced, birds, urban individuals responded more strongly than rural individuals, which is also consistent with a higher predation risk in urban habitats. Only the comparison of young, relatively inexperienced sparrows did not conform to this scenario, i.e. habitat difference was the opposite as in older birds, for which we do not have an unequivocal explanation. One possibility is that young birds might be safer from avian predators in the cities than at rural sites, when, for example, high predation pressure is strongly seasonal in urban habitats

– in this case the young urban birds captured in the autumn could be rather unexpreienced, compared to their rural conspecifics. Alternatively, in the lack of strongly developed antipredator responses, young birds' feeding latencies might have been influenced primarily by factors other than the actual predation risk. For example, their readiness to resume feeding after startle may reflect differences mostly in energy reserves, in which case the higher body mass of young rural sparrows would permit them to wait longer than the relatively smaller urban birds. However, because the scaled mass index did not differ between urban and rural birds, it is unlikely that they differed considerably in their energy reserves. Both the latter finding and the fact that the birds' response to predators was not significantly related to their scaled mass index may be due to our experimental design, i.e. we deliberately tried to minimize the differences in individuals' body condition (thus, their motivation) by allowing them to feed *ad libitum* prior their test day.

Nevertheless, the smaller body mass and size of urban birds might have affected their responses to predators independently of their energy reserves. For example, it is possible that increased body weight and thereby increased wing loading of rural birds hinder their maneuvering ability, which could reduce their willingness to take predation risk (e.g. Witter *et al.* 1994; Lind *et al.* 1999).

The reduced risk taking of urban sparrows after the attack by aerial predators such as the sparrowhawk is consistent with several observations indicating increased raptor densities in cities. The sparrowhawk is a main predator of the house sparrow, and its numbers are increasing in several urbanized habitats (Chamberlain *et al.* 2009b; Bell *et al.* 2010), reaching high densities in large European cities like Hamburg (Risch *et al.* 1996) or Prague (Kelcey & Rheinwald 2005). In Budapest (where two of our urban capture sites were located), breeding sparrowhawks are present from the early 1980s (Bagyura 1985); since then, their population has been increasing, and in 2007, the number of breeding pairs was estimated to 200 (Bérces 2007), which exceeds the breeding density of sparrowhawks in many natural habitats (Newton 1986). Furthermore, the number of sparrowhawks hunting in Budapest during winters is estimated to reach 500–600 individuals (Z. Bajor, pers. comm.). Other raptors such as the Kestrel, the Merlin (*Falco columbarius*), and the Northern goshawk also readily occupy metropolitan areas in both Europe and North America (Sodhi & Oliphant 1992; Salvati *et al.* 1999; Morandini 2006; Rutz 2006). Additionally, raptors such as the kestrel and the tawny owl (*Strix aluco*) readily adapt their diet to the altered prey species composition of cities by taking more birds, including house sparrows, than in their natural habitats (Goszczynski *et al.* 1993; Kelcey & Rheinwald 2005; Kübler *et al.* 2005). Although an interspecific comparison of birds' foraging behavior indicated reduced sensitivity to predation risk in the house sparrow compared to the more rural Spanish sparrow (*Passer hispaniolensis*), that study used only one foraging patch per species in a single suburban habitat where the two species co-occurred (Tsurim *et al.* 2008).

The higher sensitivity of urban sparrows to predation risk is also consistent with our previous results that sparrows have smaller body mass and body size in more urbanized habitats than at rural sites (see ***Chapter III***), a difference that persists in captivity for several months (Liker *et al.* 2008). This may be the result, at least in part, of selection for smaller weight on an evolutionary scale, because reduced body mass may be adaptive when the risk of predation is high (Gosler *et al.* 1995; Pérez-Tris *et al.* 2004; although other factors such as poor-quality diet in cities might also be important; see Mennechez & Clergeau 2006; Peach *et al.* 2008; ***Chapter IV***). In line with this idea, house sparrows have smaller body mass in areas with higher predation risk posed by sparrowhawks (MacLeod *et al.* 2006). Similar to these earlier findings, in our present study, rural birds were heavier than urban birds. Heavier birds may store more fat and therefore be less motivated to take the risk of predation, which might have biased the outcome of our experiment. However, differences in energy reserves are unlikely to explain the habitat differences in risk taking in our experiment, as detailed earlier.

Birds of different age and habitat might differ in their sensitivity to stress, which might have an impact on their behavioral responses. However, we did not find any significant difference in birds' body mass change related to habitat, age, or their interaction; thus, it is unlikely that differences in coping with the stress of captivity influenced our results. Differences in the level of neophobia between urban and rural birds might also influence their behavioral responses, as more complex urbanized habitats may contribute to reduced neophobia (Greenberg 2003; Echeverría & Vassallo 2008). However, we found no significant habitat *x* age interaction either in the first pre-startle latency (i.e. the bird's response to the first opening of the feeder's lid on the test day) or in the startle latency in the ground control test (i.e. the bird's response to a paper box moving on the ground). In line with these results, previous studies have found that the object neophobia of urban house sparrows is not different from, or even somewhat higher than, the neophobia of rural conspecifics (Echeverría & Vassallo 2008; Liker & Bókony 2009).

Besides the one we applied here, there are alternative methods to assess actual predation risk perceived by prey. One of these operates with the 'flight initiation distance' (FID). FID measures the distance at an animal flushes away when a potential predator or novel object approaches; hence, it is thought to be informative on predation risk in different environments as birds exposed to greater predation risk are expected to show longer FIDs (i.e. flush earlier; Stankowich & Blumstein 2005). When comparing populations of the same species, FIDs are consistently shorter in urban areas (e.g. Møller 2008). Furthermore FIDs are found to be much higher in larger-bodied, predatory species (Møller 2012). Both of these findings suggest lower predation risk in urban areas: because prey populations' tamer behavior may refer to relaxed predation pressure and also because the ubiquitous presence of humans in cities is more detrimental to predators than their prey species due to the differences in their FIDs. Thus, urban areas with high human densities may serve as refuges for prey species. However, FID is usually measured as a reaction to approaching humans (e.g. in the above studies), yet it is used as a proxy for representing general predation risk perceived by birds. This may be false if birds distinguish humans and other predators in terms of dangerousness, which can be plausible as most humans do not hunt or persecute birds in urban areas (but this can species- and region-specific, see Clucas & Marzluff 2012) opposed to e.g. sparrowhawks, cats or other predator species. Thus, whether FID is a reliable approach for assessing perceived predation risk in general still requires further investigations.

In the cat test, we did not manage to evoke anti-predator response as there was no difference in the birds' responses given to the dummy cat and its control object. One reason for this may be that cats might pose little threat for adult birds, e.g. because they may mostly catch recently fledged young. Another possible explanation could be that sparrows did not perceive the dummy as dangerous because the cat was passing by the test cage instead of moving toward the bird, and its eye-gaze direction was not focused on the cage. This is likely because both the direction of the predator's movement (Stankowich & Blumstein 2005) and their face orientation and eye-gaze focus (Hampton 1994; Watve *et al.* 2002; Carter *et al.* 2008) are known to be used as cues for risk assessment by birds. Because pet cats are regularly fed by humans and do not necessarily have to rely on hunting, it could be adaptive for sparrows to assess the actual risk by the behavior of the cat and adjust their response to it.

In conclusion, our findings do not support a reduced predation risk for urban house sparrows. The increased wariness of older, hence presumably more experienced, urban birds suggests that sparrows are more exposed to predation in cities. As our cat test was not effective, further studies are needed to investigate whether the stronger antipredatory response of urban sparrows is specific to the sparrowhawk (or raptors) or represents a more general response to predation risk.

CHAPTER VI

Quantifying the urban gradient: an easy method for broad measurements

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ABSTRACT

The process of habitat urbanization has intense and manifold effects on the biota that we need to better understand. The urbanization gradient approach is increasingly used in ecological research to study the responses of communities and populations of plants and animals to different degrees of landscape urbanization. However, the methods used for quantifying the urbanization gradient are heterogeneous. Here, first we validate a manual method designed for broad measures of landscape urbanization, based on major land-cover characteristics calculated from aerial images, that has been applied in former studies, and compare its results to measurements taken with a widely accepted geoinformatics software. Second, on the basis of this manual scoring method we introduce a recently developed, easily feasible, semi-automated method of measuring degree of urbanization, which uses only freely and worldwide accessible satellite imagery. Finally, we compare the results obtained by the three methods and the conclusions they yield within the framework of an ecological study conducted on birds. Our results show that the three methods quantify the urbanization gradient similarly, as the 'urbanization scores' they provide are strongly correlated and the results of the ecological analyses are highly repeatable across the three approaches. Since the semi-automated method grants this performance at far the lowest cost of time, we propose it as a useful tool for broad measurements of urbanization and its application can promote greater integrity between studies of urbanization effects on wildlife around the world. We also provide a download link to the free application of our semi-automated method.

Unpublished manuscript.

1. INTRODUCTION

There is an ever growing need to detect and predict the effects of changes in our environment occurring either as a result of natural processes or human activity. One of the most actual environmental changes is the escalating process of landscape urbanization. Our planet's human population is growing rapidly and alters natural landscapes at an accelerating rate throughout the world as the number and extension of urban settlements are increasing (Grimm *et al.* 2008; Hammond *et al.* 2011). The 'ecological footprint' of urban areas has become of great interest to wildlife researchers in the last decades, as urbanization turns natural landscapes into highly altered habitats with artificial surfaces, industrial pollution, anthropogenic disturbance, and severely altered energy flux and nutrient cycles (e.g. Lee 2007; McDonnell & Hahs, 2009). This phenomenon is considered to be one of the most important causes of biodiversity loss, species endangerment and extinction (Lepczyk *et al.* 2008; McKinney 2006; McDonald & Marcotullio 2011). Thus, while researchers of basic ecological science endeavour to understand the complex effects of urbanization on animal and plant communities and populations, conservation biologists seek the causes and remedies when species cannot adapt to urbanized environments (Marlzuff *et al.* 2001; McKinney 2006; Schochat *et al.* 2006). For both kinds of research, it is crucial to quantify the intensity of landscape urbanization in a way that is most relevant for the studied wildlife community or species.

Many animal-ecological studies on urbanization utilized simple comparisons of habitats labeled by various and poorly defined terms such as urban, suburban, and rural (e.g. reviewed by Marlzuff *et al.*, 2001; Theobald 2004). While this approach has the potential to reveal important differences between populations, it hinders the replication of such studies, the integration of their results, and the generalization of predictions and conservation recommendations because these terms carry different meanings in different regions of the Earth (Marzluff *et al.* 2001). Although there were suggestions for standardized terminology for categories of differently urbanized landscapes (e.g. Marlzuff *et al.* 2001), such categories are relatively broad, not necessarily relevant for the studied system and certain habitats might not even fit into any category. Instead, explicit quantitative measures of relevant landscape characteristics can provide a more useful approach. Since the introduction of the concept of urbanization gradient (McDonnell & Pickett 1990) it has become a frequently and effectively used framework for studying ecological issues of human settlements (McDonnell & Hahs 2008). The term 'urbanization gradient' refers to the spatial variation of environmental factors in relation to the intensity of urbanization, from natural landscapes to the most heavily urbanized areas (McDonnell & Hahs 2008). The simplest urban gradient would be a linear transect from the countryside to the city centre whereby the intensity of urbanization and its environmental impacts decreases monotonically with distance from the centre, but such a gradient approach would be oversimplified (e.g. McKinney 2006). Urban structures are rarely monocentric, with core regions being surrounded by asymmetric mosaics of differently urbanized landscapes such as industrial and residential outskirts (e.g. Blair 1996; McDonnell & Hahs 2008; McDonnell *et al.* 2009). In this way the urban gradient is not necessarily a geographical transect but a continuum of a combination of landscape features that vary systematically as a result of anthropogenic environmental change (McDonnell & Hahs 2008).

When quantifying urban gradients, the number of measured environmental variables can vary at a wide scale depending on the purpose of study and our desired level of precision (Hahs & McDonnell 2006). In landscape ecology for example, landscape composition (i.e. percentage of types of landscape cover) and heterogeneity (i.e. degree of contagion) are suitable predictors of ecological conditions for animals and serve as proxies for the structural characteristics of urbanization gradients (Alberti *et al.* 2001). Landscape gradients are often characterized by the proportion of areas covered by vegetation, buildings and roads (McDonnell & Hahs 2008), and these metrics often predict animal communities' species composition, abundance and species richness along the urbanization gradient (e.g. Blair 1996;

Clergeau *et al.* 1998; Germaine *et al.* 1998; Germaine & Wakeling 2001; Pillsbury & Miller 2008). This is probably because these types of landscape cover reflect components of urbanization that are crucial for a wide range of species, e.g. more vegetation may provide more sites for foraging, nesting and roosting; the number and density of buildings is probably associated with altered native vegetation, disturbance by humans and pets, noise and light pollution; and roads may increase pollution by traffic and direct mortality by collision (Miller *et al.* 2001; van der Ree 2009). The effects of these broad measures of landscape cover can be fine-tuned by more specific measures of urbanization for particular species. For example, the abundance of some bird species increases with median housing age in urban areas whereas other species show the opposite effect (Loss *et al.* 2009), and even factors as subtle as the density of trash bins can have important influence on the numbers of certain species (Jerzak 2001). Measuring such specific aspects of urbanization can be a very powerful approach to identify the mechanisms responsible for observed ecological patterns such as the loss of species richness with increasing urbanization, and thereby to aid conservation efforts. However, such data are often location-specific, difficult and/or costly to obtain, or even non-available for various study sites, limiting the extent to which studies based on fine measurements can be reproduced at or extended to different locations. In contrast, broad measures of urban gradients using land-cover features can provide a common context and integrity between urban-ecology studies throughout the world (McDonnell & Hahs 2008) while still capturing reasonably high amounts of variability in the patterns of urbanization (Hahs & McDonnell 2006).

Recently, the improving quality of remote sensing and image capturing techniques, and the increasing availability of airborne and satellite images enables these techniques to be used efficiently and extensively in biological surveys such as urban gradient measurements (e.g. Herold *et al.* 2002; Schneider *et al.* 2010). The visual processing and evaluation of such imagery help us to analyze landscape characteristics accurately with consistent methodology for different areas around the world. However, accessing sufficiently high resolution and standard aerial or satellite images is often expensive, the images from different locations are not equally available or not comparable, and evaluating them by complex geoinformatics softwares requires special expertise. To date the continental-scale monitoring policy and environmental assessments differ between the North American continent, Europe and Australia. For example, the CORINE land-cover database provides comparable digital maps of land cover for each country for much of Europe based on spectral analysis of satellite imagery (Kleeschulte & Büttner 2008). This database is widely used in national and international environmental studies, but its resolution (i.e. 25 hectares minimum mapping unit, 100 meters minimum width of linear elements) restricts its applicability for study systems that require relatively high spatial resolution. Its land-cover classes are different from the classes of the United States National Land Cover Dataset as well as from the Australian Land Cover and Land Use Dataset; furthermore, all three datasets are based on different data and different quality of satellite images (Barson *et al.* 2008; Homer *et al.* 2008). When standardized quantitative data are not available, researchers can rely on freely accessible imagery (e.g. GoogleEarth) and simple scoring methods to rank their study sites along the urban gradient (Bókony *et al.* 2010; Liker *et al.* 2008; Zhang *et al.* 2011; Zhang & Zheng 2010; ***Chapter III***). This approach provides an easy, inexpensive way of measuring urbanization, but it is very time consuming and its adequacy has not been investigated yet.

In this study our aim is to introduce and validate a quickly feasible and freely available broad method for quantifying the intensity of urbanization based on landscape cover. This recently developed method (Czúni *et al.* 2012) is a semi-automated approach based on the manual scoring system of Liker *et al.* (2008), requiring public satellite images or aerial photographs and some marginal manual work only. Using 21 study sites from an urban gradient, first we compare the 'urbanization scores' generated by both the original manual method and the newly developed semi-automated method to strictly quantitative measurements obtained by a widely accepted, expensive geoinformatics software. We also assess the measurement error of both the manual and semi-automated scoring methods. Finally, we investigate the ecological applicability of the scoring methods by repeating the analyses of a published study (***Chapter III***) using each of the three methods and testing the repeatability of results. ***Chapter III*** studied the effects of urbanization on various measures of individual health condition in a bird species, the house sparrow *(Passer domesticus)* that is undergoing population declines in several parts of the world, especially in urban areas (De Laet & Summers-Smith 2007; ***Chapter V***). The authors measured 11 indices of environmental stress on adult birds to test whether individuals in more urbanized habitats are in worse physiological state. We chose this study because it includes several ecologically relevant variables that were examined in relation to urbanization and a relatively large number of study sites (i.e. the same 21 sites we focused in this study), quantified by the manual scoring method of Liker *et al.* (2008), thus it provided a relatively large set of manual 'urbanization scores' to build upon.

2. METHODS

For the 21 differently urbanized sites studied by ***Chapter III***, we took digital aerial images from GoogleMaps (Fig. A1). Each study site was represented by a 1 km × 1 km rectangular area with the location of bird captures in the center. We quantified the intensity of urbanization from these images by three approaches as described below.

2.1. Manual scoring

We applied the manual scoring method (Liker *et al.*, 2008) on the images of 1 km × 1 km areas divided into 10 × 10 cells for each study site. We evaluated the content of each cell considering the type of three major land-cover characteristics, namely buildings (*B*), vegetation (*V*, including agricultural areas and brownfields), and paved surfaces (*R*, mostly roads and parking lots), as follows:

$$B = \begin{cases} 0 & \text{if proportion of building cover is } 0 \\ 1 & \text{if proportion of building cover is between } 0\text{ - }50\,\% \\ 2 & \text{if proportion of building cover is above } 50\,\% \end{cases}$$

$$V = \begin{cases} 0 & \text{if proportion of vegetation cover is } 0 \\ 1 & \text{if proportion of vegetation cover is between } 0\text{ - }50\% \\ 2 & \text{if proportion of vegetation cover is above } 50\,\% \end{cases}$$

$$R = \begin{cases} 0 & \text{if no paved surface is present} \\ 1 & \text{if paved surface is present} \end{cases}$$

From these cell scores we calculated the following summary land-cover measures for each study site: mean building density score (potential range 0–2), number of cells with high building density (>50% cover; range 0–100), number of cells with paved surfaces (range 0–100), mean vegetation density score (range 0–2), and number of cells with high vegetation density (>50% cover; range 0–100). For each study site, we then calculated the 'urbanization score' using the PC1 score from a principal component analysis (PCA) of the five variables described above. We will refer to this measure as manual scores henceforth.

The manual scores of the 21 study sites from ***Chapter III*** that were compiled by 3 observers (i.e. each observer scored a non-overlapping subset of the 21 sites). The PCA in ***Chapter III*** extracted one principal component (PC1) that accounted for 92.2% of the total variance and correlated strongly with reduced vegetation cover and increased density of buildings and roads. To assess the measurement error of this method, two of us (G.S. and V.B.) scored each site twice (with ca. 2 weeks between each observer's first and second scorings) and generated 2×2 sets of manual 'urbanization scores' (denoted as GS1, GS2, VB1, and VB2, respectively) by PCA (Table VI.A1). We used these scores to test the repeatability of 'urbanization scores' (i.e. the relative ranking of sites along the urban gradient) both within and between observers (see below). Furthermore, to assess measurement error at the level of image cells, we chose one suburban site situated in the middle part of the urban gradient (the Veszprém campus) and obtained manual scores for it from 10 independent observers not aware of the aims of our study, and from the two above researchers with experience in manual scoring (i.e. 12 observers in total). We used these scores to test the agreement of manual scoring between observers at the level of image cells, and to compare this to the agreement between semi-automated and manual scoring (see below). Additionally, 10 observers (including G.S. and V.B.) scored this single site twice, with at least 5 days between their first and second scoring. We used these data to test the within-observer repeatability of manual scoring at the level of image cells (see below). Note that manual scoring is very labor intensive and time consuming so re-scoring of all sites by many observers was not feasible.

2.2. Semi-automated scoring

The semi-automated scoring method, based on the approach of Liker *et al.* (2008), was developed by Czúni *et al.* (2012). This method is a trained classification method based on analysis of several image features; its aim is to greatly reduce the time required for scoring while retaining as much precision as possible.

First we created the appropriate general classification model which ultimately generates the cell scores for *B*, *V* and *R* categories (Fig. VI.1). We took satellite images in .jpeg format from GoogleMaps of the 1 km × 1 km areas studied by ***Chapter III***. Since these satellite images have different resolution, we normalized image size for 164 cm/pixel, and divided each image to 100 image cells; these cells served as the units of analysis for the classifications (100 × 100 m of physical terrain size). We took the 21 sites in the order as ranked by the manual scores of ***Chapter III*** and chose every second image to represent the entire urban-rural gradient. For these selected images we extracted relevant image features by image processing methods to obtain high-dimensional data vectors for our classification models. For each image cell we measured the values of 52 different features based on colour, texture, and local contrast (edges and corners) information, as described in detail by Czúni *et al.* (2012). Briefly, we calculated the following features: number of edge points detected by the Canny edge detector (Canny 1986) applied in 19 different settings (19 values); number of points belonging to each of the 5 specified segment classes: grass, tree/bush, building, road, others, with 4 different window size settings of the Laws classifier (20 values; Laws 1980); number of corner points detected by the Harris corner detector (Harris & Stephens 1988) applied in 6 different settings (6 values); average value of Red, Green and Blue channels within a block (3 values), average and modus of Hue (of the HVS colour space), and the corresponding variance of Hue (4 values).

Finally, we established the relation, by three independent classification models, between the high-dimensional data vectors and the cell scores obtained by manually scoring the values of *B*, *V* and *R*, respectively. For this purpose, we used a set of manual scores (GS3) by a single observer (G.S.) who has extensive practice with manual scoring. For the classification task we used the Support Vector Machine (SVM) algorithm (Vapnik 2006), which is a robust classification and regression technique that maximizes the predictive accuracy of a model without overfitting the training data. After establishing the models (i.e. training), we used the remaining images to compare the manually assigned scores with the scores predicted by the SVM model (i.e. testing).

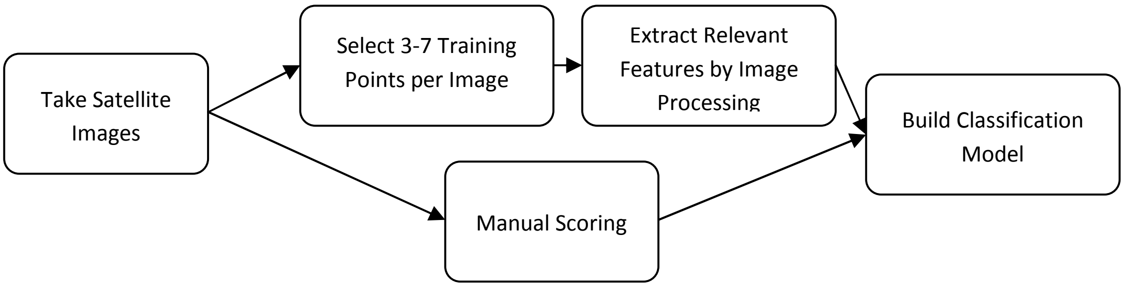


Fig. VI.1. Process of the building of the classification model in the semi-automated scoring method.

Once the classification model is established, it can be used to generate the 'urbanization scores' for other areas the user wishes to study (Fig. VI.2); here we simply applied the SVM model to the 21 images (100% of cells) we had used for training and testing the model. As landscape objects of the same type can highly vary in appearance both within and between images (e.g. buildings may look very different), we improved the SVM model's classification efficiency by adapting the Laws classifier with manually selecting a very few, typically 1-5, training points for each of the three major land-cover characteristics (*B*, *V* and *R*) per image. Then we predicted the values of *B*, *V* and *R* for each cell by applying the three respective SVM models, calculated the five summary land-cover measures of Liker *et al.* (2008) from the predicted values of *B*, *V* and *R*, and used them in a PCA to obtain the 'urbanization score' (Table VI.A1). We will refer to the 'urbanization scores' gained from this measure as semi-automated scores henceforth.

Our classification models obtained by the above training process can be used to generate the semi-automated scores of urbanization for any 1 km × 1 km area by our application, which can be downloaded freely, along with a user's guide and the Czúni et al. (2012) paper, from the following URL: https://www.dropbox.com/sh/i9ik1novs680xbz/PYv0k7XqwE

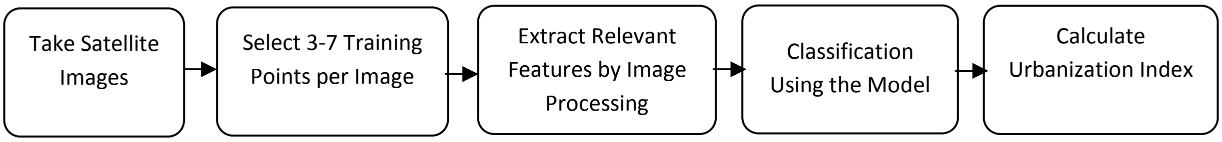


Fig. VI.2. Process of calculating 'urbanization score' in semi-automated scoring method.

2.3. Geoinformatics measurements

To obtain strictly quantitative measurements of land-cover characteristics of each study site, we conducted measurements using the ArcGIS 10.0 (ESRI 2010) geoinformatics software. All measurements were done by a single person who had previous experience with ArcGIS and was not aware of the aims of our study. In each image all polygons of landscape objects were traced and categorized as vegetation, buildings, paved surfaces, or other (e.g. railways, water bodies). Then we calculated the total percentage area of each cover type by summing the area of the polygons of each of the four categories. Finally, we extracted an 'urbanization score' from a PCA including the percentage cover of the three relevant categories (i.e. vegetation, buildings, and paved surfaces; Table VI.A1).We will refer to this measure as 'ArcGIS scores' henceforth. For certain analyses, we converted the proportion of cover by buildings, vegetation and paved surfaces for each cell into values of 0, 1, or 2 according to Liker *et al.* (2008).

2.4. Data analysis

We assessed the measurement error of both scoring methods by several approaches. For the manual scoring, first we tested the agreement within and between observers at the level of image cell scores for the Veszprém campus site using the kappa statistic, i.e. Cohen's kappa with squared weights for the agreement between two sets of scores by the same observer (n=10), and Fleiss' kappa for the agreement between observers (n=12 ; Peat, 2002). We express the level of agreement as the % of cells receiving the same score from the observer's 1st and 2nd scoring (within-observer repeatability) for each observer, and the % of cells receiving the modal value of the 12 observers' 1st scores for that cell (between-observer repeatability).

Second, we tested the repeatability of the manual scoring at the level of images (sites) both within and between observers (i.e. 'urbanization scores' GS1, GS2, VB1, and VB2) by calculating the intra-class correlation coefficient (ICC, see below) between each pair of 'urbanization scores'. We also tested the repeatability between these scores and the original urbanization scores of ***Chapter III*** which were compiled by 3 observers.

Third, we evaluated the agreement between the manual scores and the semi-automated scores in multiple ways. We measured the performance of the classification model by the % of correctly classified cells during both the training (i.e. the first half of the images) and the testing (i.e. the other half of the images) phase, and by calculating the area under the ROC (receiver operator characteristic) curve. The ROC curve plots the proportion of true positive classifications in relation to the proportion of false positive classifications; the area under this curve is 1 for perfect models and 0.5 when classification is random. Then we tested the agreement between the semi-automated scores and the manual scores on which the classification model was built on (GS3) both at the level of cells for the Veszprém campus site (Cohen's kappa) and at the level of images of all sites (ICC). We also tested the repeatability between the semi-automated scores and the other sets manual scores (GS1, GS2, VB1, and VB2).

Finally, we compared the 'urbanization scores' generated by the manual method (i.e. the original manual scorings of ***Chapter III***, GS1, GS2, GS3, VB1, and VB2) and the newly developed semi-automated scoring method to those extracted from the ArcGIS measurements, at the level of sites, using ICC. We did not assess the error of the ArcGIS method as we treated this as a "yardstick" for relatively accurate quantification of landscape cover.

To investigate the ecological applicability of the scoring methods we repeated the analyses of ***Chapter III*** that tested the effects of landscape urbanization on birds' body condition, and then we compared the results. In short, we used linear mixed-effect (LME) models that contained each of the 11 measures of environmental stress as dependent variable, 'urbanization score' and various confounding variables as predictors, and capture site as random factor to control for the non-independence of individuals captured at the same site. Then we reduced the initial models by backwards stepwise selection, omitting the effect with the highest P-value step by step until only significant ($P<0.05$) effects remained, but never excluded our predictor of interest, i.e. urbanization and the random factor (for more details on data analysis see ***Chapter III***). We ran the models with 'urbanization scores' provided either by the semi-automated scoring method or by ArcGIS measurements, and compared the results with those published in ***Chapter III*** based on their manual scores. We took the parameter estimate for 'urbanization score' from each of the 11 models and tested the repeatability (ICC) over the three approaches pair-wise.

Statistical analyses were run in R 3.0.1, using the 'icc' function of the 'irr' package for calculating the ICC, with 95% confidence intervals. The ICC approach tests for repeatability by expressing the proportion of variance in a character (e.g. 'urbanization score') that occurs among rather than within groups (e.g. different methods or different observers); for further details see Lessells & Boag (1987).

3. RESULTS

3.1. Agreement at the image cell level

By investigating within-observer repeatability, we found that the manual scores for image cells of the Veszprém campus site showed high agreement between the first and second scorings of the 10 observers, including 8 observers who had no previous experience with the manual scoring method (Table VI.1a; p<0.012 for all kappa tests). As for between-observer repeatability, the percentage of 12 obsevers assigning the modal value (i.e. the most frequently assigned score) for a cell averaged 70-90% for the 100 cells, showing that most observers agreed significantly on the scores of most cells (Table VI.1b; p<0.001 for all kappa tests). Between-observer repeatability for each land-cover type varied with the amount of cover, as measured in ArcGIS, in each cell (Fig. VI.A2). For buildings we found the highest uncertainty of manual scoring (i.e. the lowest % of agreement with the modal value) for cells with intermediate cover (ca. 20-30% of buildings per cell), whereas for vegetation and paved surfaces the observers agreed the least when cell cover was close to zero (Fig. VI.A2).

The agreement between the semi-automated scores and the manual scores used for training classifier (GS3) was also significant for the Veszprém campus site (Table VI.1c; p<0.001 for all kappa tests) and was comparable to the agreement between manual scores of different observers (see Table 1b). Overall, the performance of the classification models for the three land-cover categories for the 21 × 100 cells (i.e. all sites) was around 80% during both the training and the testing phase of the semi-automated method (Table VI.2). The area under the ROC curve was higher than 0.7 in each case, showing that the expected performance of the SVM classifiers was appropriate for our purposes (Table VI.2).

3.2. Agreement at the 'urbanization gradient' level

The 'urbanization scores' for the full set of 21 sites gained by the repeated manual scorings of two observers (GS1–GS2 and VB1–VB2) showed very high within-observer repeatability (Table VI.3) as can be seen from the remarkable overlap of points along the y axis on Fig. VI.3a. For vegetation, both observers attained the highest repeatability for the least urbanized sites with high vegetation cover (Fig. VI.A3), whereas for buildings and paved surfaces they were the least consistent when scoring sites with intermediate urbanization (Fig. VI.A3).

The between-observer repeatability amongst the manual 'urbanization scores' by G.S, V.B. and ***Chapter III*** was high and significant in all comparisons (Table VI.3; Fig. VI.3a). Repeatability was also high and significant between the 'urbanization scores' yielded by the semi-automated method and the various manual scorings (Table VI.3; Fig. VI.3b), and between the ArcGIS measurements and all manual and semi-automated scorings (Table VI.3; Fig. VI.3c). The agreement between the manual scores of ***Chapter III*** and the scores calculated from ArcGIS measurements was highest when vegetation cover was high and the cover of buildings and paved surfaces was either very small or very large (Fig. VI.A4).

Table VI.1. Agreement of scores across 100 cells for the Veszprém campus site.

	buildings (B)	vegetation (V)	paved surfaces (R)
(a) Repeatability within observer (% of agreement)	-	-	-
Observer KD	99	99	97
Observer GS	95	93	96
Observer CL	96	93	82
Observer LA	80	83	100
Observer VPZ	90	74	91
Observer NGA	80	84	88
Observer AGY	76	75	92
Observer GM	70	73	95
Observer SZG	70	73	95
Observer VB	64	68	86
Average of 10 observers	**83**	**82**	**93**
(b) Repeatability between 12 observers (% assigning the modal value)	**70**	**74**	**91**
(c) Repeatability between semi-automatic and manual cell scores (GS3)	**67**	**69**	**91**

Table VI.2. Overall accuracy of the *B, V* and *R* classification models in the semi-automated scoring method.

	Training	Testing	Area under the ROC curve (±SE)
Building	82.09%	80.1%	0.734 ± 0.050
Vegetation	86.09%	76.7%	0.746 ±0.062
Road	84.45%	86.3%	0.708 ±0.090

3.3. Agreement of ecological results

Models of avian body condition containing different urbanization scores yielded qualitatively identical results for each of the body condition indices investigated (Fig. VI.4; see the details of the final models in Table VI.A2). Parameter estimates for the effect of urbanization were highly repeatable between the manual scores of ***Chapter III*** and both the semi-automated scores (ICC=0.838, p<0.001, N=21) and the ArcGIS scores (ICC=0.938, p<0.001, N=21). There was a somewhat lower but still highly significant repeatability between the semi-automated scores and ArcGIS scores (ICC=0.73, p=0.003, N=21; Fig. VI.4).

Table VI.3. The intra-class correlation coefficients (ICC) between 'urbanization scores' obtained by various methods. For all comparisons, $p < 0.001$

	Chapter III	GS1	GS2	VB1	VB2	semi-automated	ArcGIS
Chapter III	--	0.994	0.991	0.986	0.988	0.979	0.970
GS1	0.994	--	0.997	0.988	0.988	0.985	0.958
GS2	0.991	0.997	--	0.987	0.989	0.976	0.955
VB1	0.986	0.988	0.987	--	0.998	0.96	0.972
VB2	0.988	0.988	0.989	0.998	--	0.958	0.977
semi-automated	0.979	0.985	0.976	0.96	0.958	--	0.925
ArcGIS	0.970	0.958	0.955	0.972	0.977	0.925	--

Fig. VI.3. Agreement of 'urbanization scores' for 21 sites (a) between various manual scores, (b) between the semi-automated and manual scores, and c) between ArcGIS, semi-automated, and manual scores. The line stands for perfect agreement (i.e. y=x).

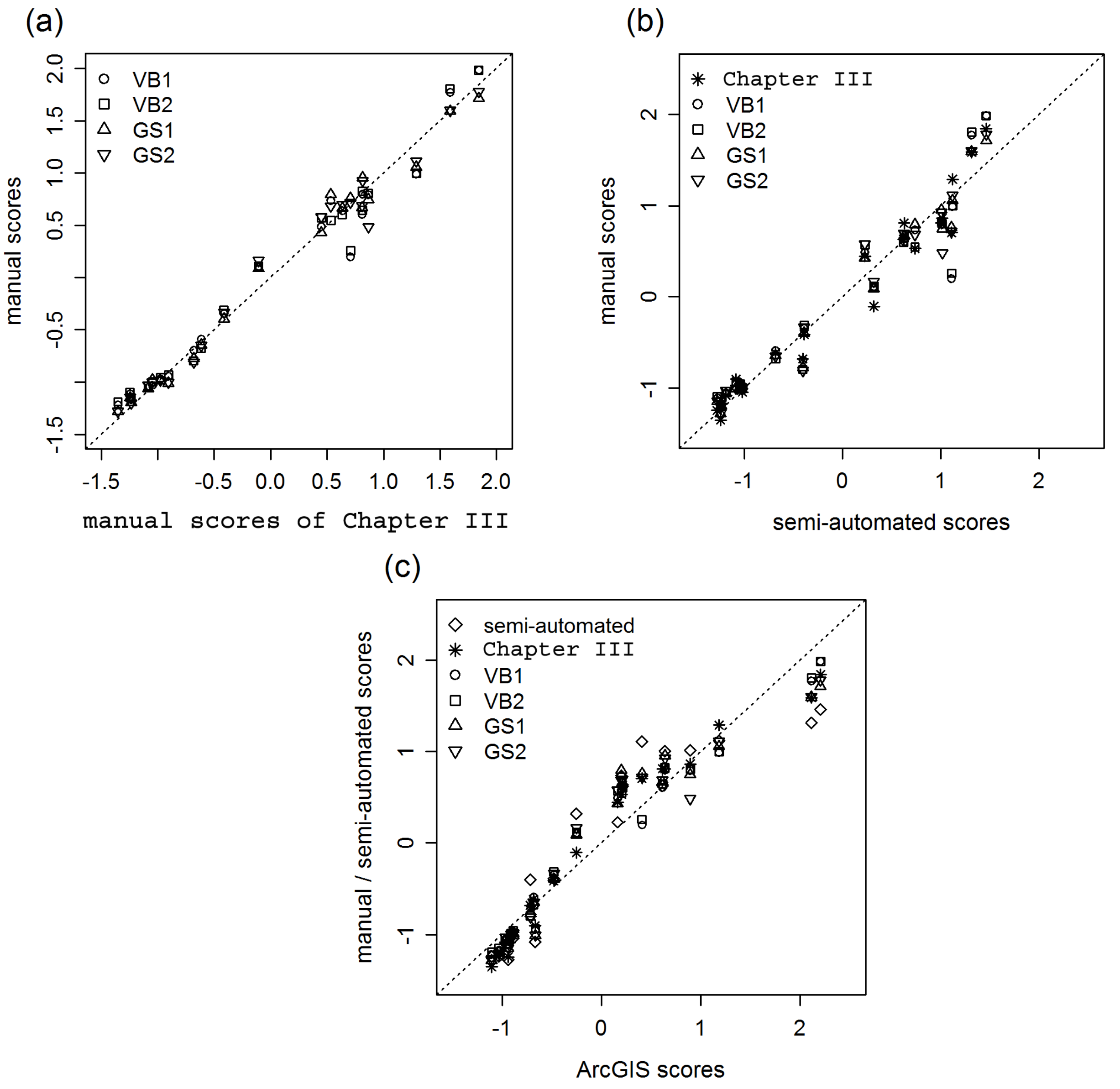
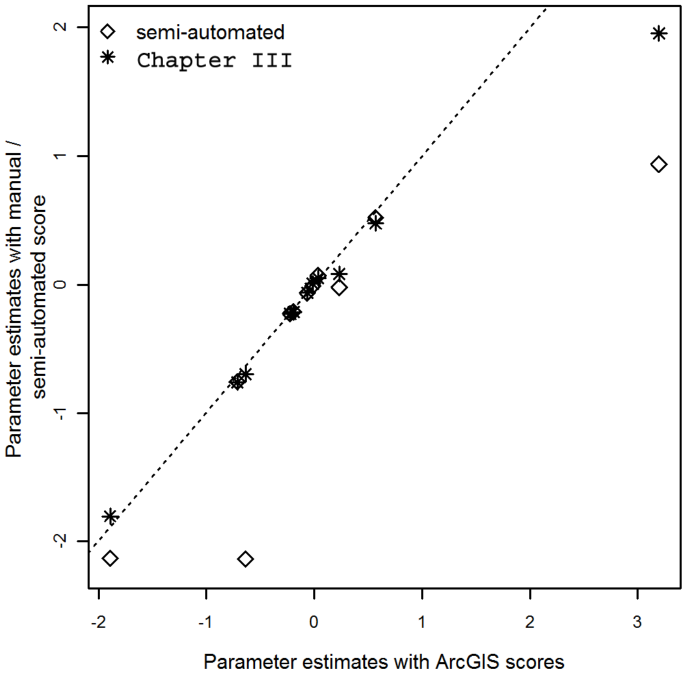


Fig. VI.4. Agreement of parameter estimates for the effect of urbanization on various measures of bird health from LME models including 'urbanization scores' generated by manual or semi-automated scoring or ArcGIS measurements (see Appendix: Table VI.A2). The line stands for perfect agreement (i.e. y=x).



4. DISCUSSION

The study of urbanization gradients has been a quite popular research area in the latest decade, and such studies use a great variety of methods to quantify the intensity of urbanization. Here we compared three broad approaches within the framework of an ecological problem to assess the reliability and applicability of two scoring methods against well-accepted geoinformatics measurements. Although several similar approaches and global maps have been applied to quantify differences across urban-rural gradients using remote-sensing data (e.g. Arino *et al.* 2007; Bartholome & Belward 2005; Elvidge *et al.* 2007; Imhoff *et al.* 1997; Schneider *et al.* 2010; Sexton *et al.* 2013), finding a globally applicable way of measuring land-cover features on a relatively fine scale remains a challenge. Global maps usually have coarse spatial resolution (mostly 1-2 km) and their applicability varies across differently developed regions (reviewed by Schneider *et al.* 2010), whereas databases with finer spatial resolution (e.g. 30-300 m) are typically specific to certain regions or time intervals or study systems (e.g. Arino *et al.* 2007; Prins *et al.* 2005; Sexton *et al.* 2013). Within each of these frameworks, urbanized areas are represented as a function of different features such as population numbers, nighttime lights, and satellite-derived land-cover classes; resulting in inconsistencies in how they depict the urban landscape (Schneider *et al.* 2010). The approach we propose here offers a simple alternative for quantifying relative levels of urbanization in a standardized way in whatever region of the Earth at fine spatial scale, and allows researchers to flexibly choose the type of landscape features without depending on national land-cover datasets and regionally specified parameters. As a starting step, here we examined the performance of this approach using a particular setup of ca. 1.6 m resolution and 3 major land-cover types within one "urban ecoregion" (Schneider *et al.* 2010).

First we evaluated the manual scoring method introduced by Liker *et al.* (2008). Although this method has been applied in a handful of studies (Bókony *et al.,* 2010; Liker *et al.* 2008; Zhang *et al.* 2011; Zhang & Zheng 2010; ***Chapter III***), its validity had not been addressed empirically. The main advantages of the manual scoring method are its very simple classification rules with large tolerance ranges and its easy applicability to any kind of aerial image of study areas, including freely accessible GoogleMaps images. However, its results are inevitably prone to the subjective evaluating decisions made by different observers during the process of classifying the land-cover contents of each image cell. Here we have shown that there is indeed considerable variation both within and between observers when assigning the values of 0, 1 or 2 to the same set of image cells, especially when the amount of land-cover to be evaluated in a given cell is intermediate (for buildings) or small (for vegetation and paved surfaces). This variation well reflects the different and sometimes inconsistent cognitive classification rules applied by the observers; for example, small and/or scattered patches of vegetation or paved surfaces covered by canopy can be easily missed from consideration. Similarly to this, estimating whether total building cover is below or above 50% in an image cell (resulting in classification value of 1 or 2) proved to be the hardest task for observers when scoring cells with intermediate amounts of building cover.

Despite these uncertainties at the image-cell level, however, we have found that the manual scoring method is still a robust way of assessing the degree of urbanization of sites across different landscapes. First, at image cell level, the agreement both within and between observers was often high, indicating that despite the above mentioned uncertainties, even completely inexperienced people agree more than they differ when scoring the same image cells. With some practice, one can reach >90% repeatability as shown by the re-scorings of G.S. in this chapter, but similar accuracy can also be achieved by inexperienced observers (see Table VI.1a). Second, and more importantly, the repeatability between the 'urbanization scores' generated for the same set of 21 sites by different observers was very high, demonstrating that they ranked the sites similarly with respect to urbanization. Since the goal of the scoring method is to provide a relative measure of urbanization, its validity ultimately depends on its performance at the level of sites. Different observers, or even the same person at different times, can differ in their cognitive rules by which they assign cell scores, but as long as they are consistent in these rules across sites, they will still produce consistent scores for placing the sites along the gradient, as shown by the >98% repeatabilities of manual ‘urbanization scores’. Finally, the various manual scores of urbanization were also highly repeatable with the scores generated from the more objective and accurate measurements taken with ArcGIS, suggesting that the human eye is fairly effective in assessing the amount of cover by vegetation, buildings and roads overall across images.

Having found that the manual scoring method is suitable for quantifying the urban-rural gradient, our next goal was to find and validate a less labour-intensive alternative. The manual scoring requires at least one order of magnitude less time than the precise measurements with ArcGIS (for example, measuring a complex urban site takes ca. 10-12 hours with ArcGIS and ca. 1 hour with the manual scoring); however, the manual method still gets quite time-consuming as the number of study sites increases. Also, more scoring probably leads to decreasing performance due to its monotony and the accumulation of human errors such as overlooking small details or mistyping the assigned values. Therefore we took the approach of Czúni *et al.* (2012) who developed the semi-automation of the manual scoring method, with fewer subjective errors and significantly less time required. Finding an appropriate approach to quantify urbanization based on automatic visual processing is challenging, since pixel-based algorithms are not effective enough due to the high variability in the visual appearance of an object type, depending on image resolution, season of the year, time of the day, prevailing weather, type of vegetation and building structure, etc. (Czúni *et al.* 2012). Thus, the semi-automated scoring method classifies image blocks instead of pixels, following the logic of the manual scoring, based on 52 visual features. Here we have shown that this method replicates the manually assigned cell scores similarly well as non-trained humans’ scores agree with each other, and the ‘urbanization scores’ for the study sites are highly repeatable between the semi-automated method and 5 different sets of manual scoring. Furthermore, the semi-automated scores of urbanization were also highly repeatable with the scores from the more precise, polygon-based ArcGIS measurements. For both manual and semi-automated scores, we found that the agreement with ArcGIS scores was the highest for roads (Fig. VI.A2 & VI.A4), probably because determining the presence or absence of paved surfaces is the easiest task during the land-cover classification process. We found the poorest agreement at sites with intermediate urbanization, probably due to the difficulties in scoring image cells containing several buildings interspersed with patches of vegetation and other land-cover objects, as detailed above. The slightly sigmoid-like relationship on Fig. 3c is likely a reflection of the difference between the scoring methods and ArcGIS, i.e. intermediate cover may be overestimated and very large cover may be underestimated by the simplifying rules of image-cell scoring; however, these differences had little impact as the repeatability of ‘urbanization scores’ was >90% between ArcGIS and both scoring methods.

As a final step of validating both the manual and the semi-automated scoring methods, we used the ‘urbanization scores’ generated by each method for the 21 study sites of ***Chapter III*** and repeated their analyses to investigate the effects of landscape urbanization on the body condition of adult house sparrows. We found that, in all 11 analyses of body condition indices, both the semi-automated method and the ArcGIS measurements yielded qualitatively the same results as the manual method, i.e. the predictor variables retained in the final models and whether or not they had significant effects were identical to the results of ***Chapter III***. Furthermore, the three different scores of urbanization received very similar parameter estimate values in most cases, as demonstrated by the high and significant repeatabilities among them. There were only two cases in which the three methods yielded relatively different parameter estimates; however, there was no bias between the three methods as the semi-automated scoring under-estimated the effect of urbanization in one case and over-estimated it in the other compared to the other two methods. We do not know the reason for this difference, but since both dependent variables were plumage coloration traits (bib size and wing bar size) we might speculate that measurement error might have been higher for these traits than for the rest of the body condition indices. Nevertheless, due to the higher uncertainty of these estimates the result was qualitatively unaffected, suggesting that the power of these two analyses might have been limited anyway. In analyses with obviously high power (i.e. scaled mass index, body mass, tarsus length), the three methods resulted in almost exactly the same parameter estimate values for urbanization.

Thus, we propose that the semi-automated scoring method is a reliable tool for standardized and time-efficient quantification of urban gradients, and it is open for further development to test and improve its applicability to a greater variability of landscape types. Firstly, since all the areas studied to develop (see Czúni *et al.* 2012) and ecologically validate our semi-automated method are located in Hungary, Europe, it remains to be seen how well the method can be applied to other geographical regions. Although our study sites represent a very wide range of the urbanization gradient from almost 100% vegetation to almost 100% building cover (see Fig. VI.A1), there are very different landscape compositions in other parts of the world, with diverse city structures and types of buildings and vegetation. The classification models we built here are likely to work well for landscapes similar to ours and can be applied to score such new sites with our software, however, they might not be suitable for study sites looking very differently from ours; for such sites the semi-automated method should be trained and tested with manual scores obtained for those sites. Secondly, although we tested our method's applicability in the context of avian ecology, we propose it to be useful in other study systems. As different types of landscape features could be relevant for different organisms (e.g. Croci *et al.* 2008), incorporating further types of landscape cover into the classification process may be necessary, e.g. separating woods from other types of vegetation, or including water bodies, railways, construction areas, golf courses, rubbish-shoots, etc. Furthermore, while our method works well with study areas of 500 m × 500 m (Czúni *et al.* 2012) and 1 km × 1 km (this study) and images with pixel size of 164 cm, this spatial scale and resolution may be inappropriate for some study systems such as organisms with very small size and/or limited home range. Validating the method for much smaller or larger areas and study sites of variable size may further extend the method's applicability. With these future improvements our method could be useful for investigating a wide spectrum of animal taxa and research questions related to landscape urbanization.

To sum up, we have demonstrated that both the manual scoring method of Liker *et al.* (2008) and the semi-automated scoring method of Czúni *et al.* (2012) can be used to reliably quantify the intensity of urbanization along the urban-rural gradient. Both methods generated scores of urbanization that ranked the study sites along the gradient in a way that is consistent with more objective and precise geoinformatics measurements, and all three methods allowed for the same biological conclusions in a study of bird health indices. Thus, we propose that the semi-automated scoring method is a powerful tool for broad studies of urbanization, because it provides reasonable accuracy while it does not require expensive imagery and software, it is easy to use and, perhaps most importantly, allows researchers around the world to apply a standardized methodology for quantifying urbanization. This method can be used in any study that does not aim to investigate or predict the effect of the exact amount of various land-cover types within habitats, such as basic ecological research and even certain areas of conservation biology and landscape planning. With further development, the semi-automated method can be expanded to include other types of land-cover features and apply to other spatial scales than those studied here. Therefore this methodology has the potential to provide a common context and greater integrity between urbanization studies conducted at different locations of the Earth, thereby helping us to draw better general conclusions about the impacts of urbanization on the world around us.

5. SUPPLEMENTARY MATERIAL TO CHAPTER VI

Fig. VI.A1. Images of the 21 study sites, dowloaded from GoogleMaps on 27 March 2012.

Bánd Budapest, ÁOTK campus Budapest, Kőbánya-Kispest

Budapest, Lurdy Ház Budapest, Hunyadi tér Budapest, Zoo

Csepel Dunakeszi, Alag Hajmáskér

Hortobágy

Nemesvámos

Salföld

Székesfehérvár

Szentgál

Üllő, Dóramajor

Várpalota

Veszprém, Cholnoky ltp.

Veszprém, Hotel

Veszprém, campus

Veszprém, Zoo

Vilmapuszta

Fig. VI.A2. Agreement of manual cell scores by 12 observers, in relation to % of the respective type of cover in that cell as measured with ArcGIS for the Veszprém campus site. Agreement is expressed as the % of observers that assigned the modal value to the respective cell. Lines are fitted LOESS lines.

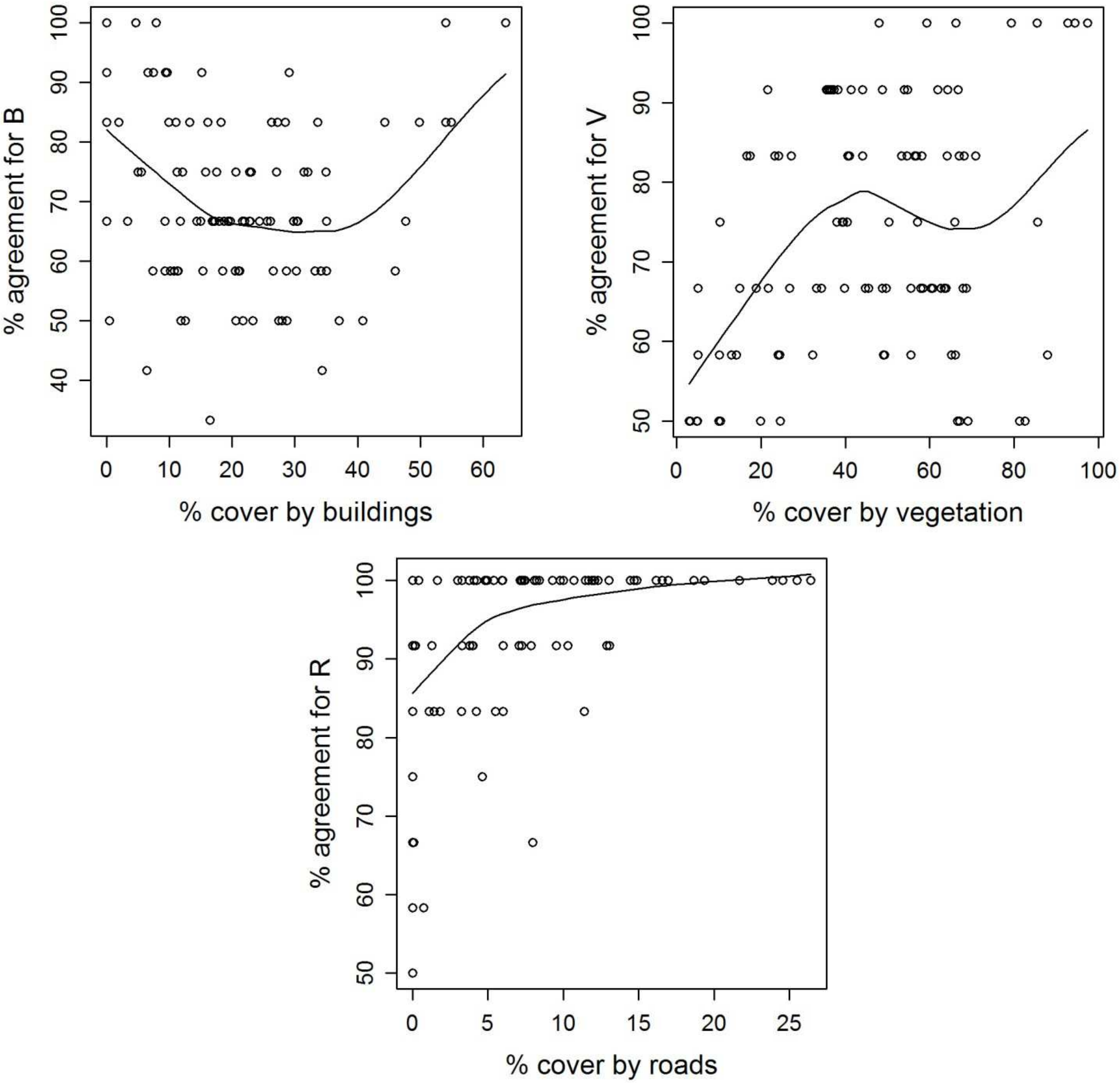


Fig. VI.A3. Within-observer agreement of manual urbanization scores for each site, in relation to the urbanization score of sites calculated from the observer's first scoring. Agreement is expressed as the % of cells (out of 100 cells per image) assigned the same manual score twice by the respective observer. Lines are fitted LOESS lines.

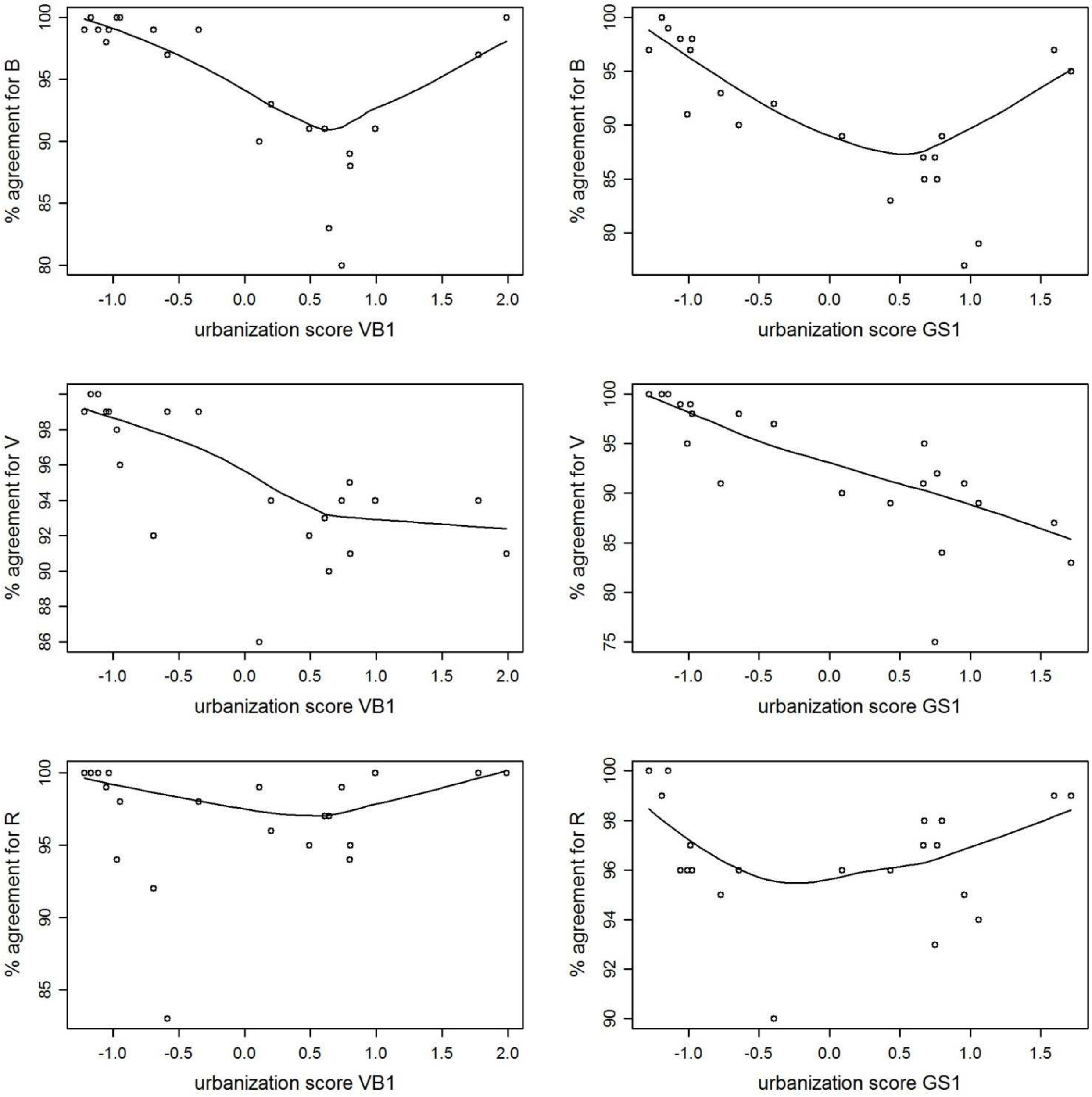


Fig. VI.A4. Agreement between the manual scoring by Bókony et al. (2012) and ArcGIS measurements. The *x* axis shows the total % of the respective land-cover category at the image level, as measured in ArcGIS; on the *y* axis the agreement is expressed as the % of cells (out of 100 cells per image) receiving the same cell score in the manual scoring and in the ArcGIS measurements. Lines are fitted LOESS lines.

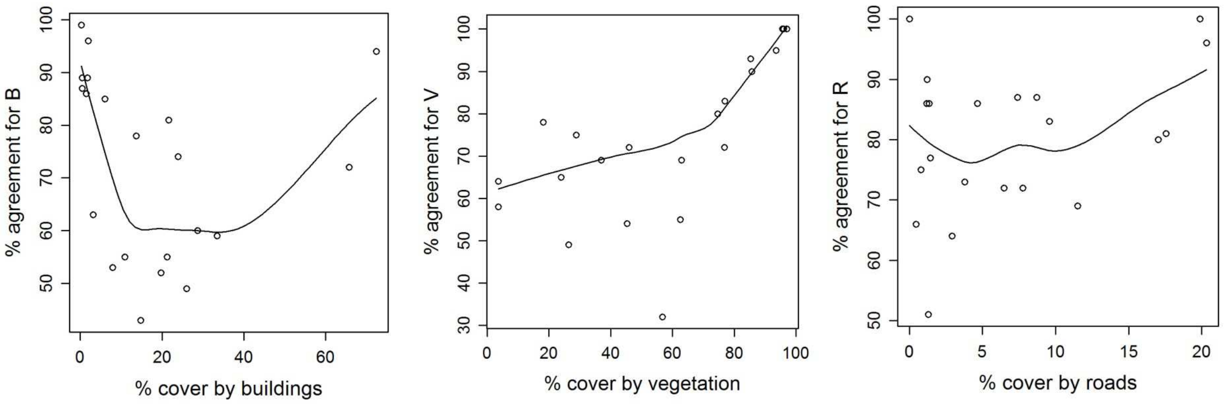


Table VI.A1. PCA results for various scoring methods.

PCA loadings	Number of cells with roads	Mean building density	Mean vegetation density	Number of cells >50% buildings	Number of cells >50% vegetation	Eigen-value	Explained variance %
Manual (VB1)	0.95	0.98	-0.98	0.82	-0.97	4.43	88.64
Manual (VB2)	0.94	0.97	-0.98	0.76	-0.97	4.30	85.96
Manual (SG1)	0.96	0.98	-0.98	0.95	-0.98	4.72	94.47
Manual (SG2)	0.96	0.98	-0.98	0.94	-0.98	4.70	94.01
Manual (SG3)	0.98	0.99	-0.98	0.97	-0.99	4.81	96.11
Semi-automated	0.97	0.99	-0.98	0.97	-0.99	4.85	97.01
ArcGIS[1]	0.93	0.93	-0.96	0.77	-0.96	4.18	83.61
ArcGIS[2]	0.97	0.96	-0.96			2.79	92.96

[1] Proportion of cover by buildings, vegetation and paved surfaces for each cell was converted into values of 0, 1 or 2, according to Liker *et al.* 2008.

[2] Proportion of cover by buildings, vegetation and paved surfaces for each site was used in the PCA.

Table VI.A2. Final LME models of birds' body condition indices with the manual (***Chapter III***), semi-automated and ArcGIS urbanization scores. The number of birds and sites used: [1]: 37, 9; [2]: 35, 9; [3]: 85, 12; [4]: 147, 10; [5]: 41, 8; [6]: 144, 10; [7]: 1695, 21; [8]: 1695, 21; [9]: 1809, 21; [10]: 314, 7; [11]: 169, 10.

	Explanatory variables	Manual scores		Semi-automated scores		ArcGIS scores	
		b ± SE	**P**	**b ± SE**	**P**	**b ± SE**	**P**
Corticosterone levels (ng/ml)	Baseline[1]	−	−	−	−	−	−
	Intercept	3.47 ± 0.34	−	3.47 ± 0.34	−	3.48 ± 0.34	
	Sex (male vs. female)	3.19 ± 0.89	0.001	3.19 ± 0.89	0.001	3.18 ± 0.89	0.001
	Urbanization	0.05 ± 0.41	0.903	0.07 ± 0.36	0.852	0.03 ± 0.52	0.949
	Stress−induced[2]	−	−	−	−	−	−
	Intercept	43.37 ± 1.60	−	43.55 ± 1.58	−	43.31 ± 1.63	−
	Urbanization	−1.80 ± 2.10	0.418	−2.13 ± 1.81	0.278	−1.89 ± 2.55	0.481
Hematocrit (%)	Winter[3]	−	−	−	−	−	−
	Intercept	57.40 ± 0.54	−	57.33 ± 0.54	−	57.30 ± 0.54	
	Urbanization	0.08 ± 0.61	0.896	−0.02 ± 0.61	0.975	0.23 ± 0.63	0.724
	Molting season[4]	−	−	−	−	−	−
	Intercept	74.07 ± 10.88	−	73.89 ± 10.88	−	73.45 ± 10.83	−
	Molt stage	0.66 ± 0.19	<0.001	0.66 ± 0.19	<0.001	0.66 ± 0.19	<0.001
	Date	−0.11 ± 0.04	0.039	−0.11 ± 0.04	0.04	−0.11 ± 0.04	0.04
	Age (older vs. young)	0.004 ± 0.82	0.997	−0.06 ± 0.82	0.939	−0.01 ± 0.82	0.993
	Urbanization	0.48 ± 0.47	0.346	0.52 ± 0.48	0.317	0.57 ± 0.55	0.335
	Age × urbanization	−1.15 ± 0.54	0.035	−1.23 ± 0.56	0.03	−1.3 ± 0.61	0.034
H:L ratio	Winter[5]	−	−	−	−	−	−
	Intercept	0.22 ± 0.12	−	0.22 ± 0.12	−	0.21 ± 0.16	−
	handling time	0.005 ± 0.002	0.061	0.005 ± 0.002	0.05	0.005 ± 0.002	0.048
	Urbanization	0.009 ± 0.083	0.922	0.01 ± 0.07	0.892	−0.012 ± 0.099	0.906
	Molting season[6]	−	−	−	−	−	−
	Intercept	0.16 ± 0.05	−	0.15 ± 0.05	−	0.15 ± 0.05	−
	handling time	0.002 ± 0.001	0.011	0.002 ± 0.001	0.011	0.002 ± 0.001	0.009
	Urbanization	−0.06 ± 0.02	0.019	−0.07 ± 0.02	0.02	−0.066 ± 0.02	0.021
Scaled mass index[7]	Intercept	28.49 ± 0.19	−	28.49 ± 0.19	−	28.49 ± 0.19	−
	Date	−0.002 ± 0.001	<0.001	−0.002 ± 0.001	<0.001	−0.002 ± 0.001	<0.001
	Time of day	0.003 ± 0.001	<0.001	0.003 ± 0.001	<0.001	0.003 ± 0.001	<0.001
	Sex (male vs. female)	−0.39 ± 0.10	<0.001	−0.39 ± 0.10	<0.001	−0.39 ± 0.10	<0.001
	Urbanization	−0.22 ± 0.16	0.205	−0.21 ± 0.16	0.218	−0.19 ± 0.17	0.268
Body mass[8]	Intercept	28.50 ± 0.15	−	28.50 ± 0.15	−	28.50 ± 0.16	−
	Date	−0.003 ± 0.001	<0.001	−0.003 ± 0.001	<0.001	−0.002 ± 0.001	<0.001
	Time of day	0.003 ± 0.001	<0.001	0.003 ± 0.001	<0.001	0.003 ± 0.001	<0.001
	Sex (male vs. female)	−0.68 ± 0.09	<0.001	−0.69 ± 0.09	<0.001	−0.68 ± 0.09	<0.001
	Urbanization	−0.76 ± 0.12	<0.001	−0.76 ± 0.12	<0.001	−0.71 ± 0.14	<0.001
Tarsus length[9]	Intercept	19.02 ± 0.04	−	19.02 ± 0.04	−	19.02 ± 0.04	−
	Sex (male vs. female)	−0.13 ± 0.04	<0.001	−0.13 ± 0.04	<0.001	−0.13 ± 0.04	<0.001
	Urbanization	−0.23 ± 0.04	<0.001	−0.22 ± 0.04	<0.001	−0.22 ± 0.05	<0.001
Bib size (mm2)[10]	Intercept	179.99 ± 43.74	−	181.97 ± 43.55	−	178.16 ± 43.2	−
	Date	0.27 ± 0.07	<0.001	0.26 ± 0.07	<0.001	0.27 ± 0.07	<0.001
	Body mass	4.03 ± 1.44	0.006	3.98 ± 1.44	0.006	4.09 ± 1.43	0.004
	Urbanization	1.95 ± 6.22	0.766	0.94 ± 6.11	0.884	3.19 ± 5.56	0.59
Wing bar size (mm^2)[11]	Intercept	46.14 ± 40.80		51.87 ± 40.68	−	44.63 ± 40.25	−
	Date	0.13 ± 0.07	0.048	0.13 ± 0.07	0.05	0.13 ± 0.07	0.044
	Sex (male vs. female)	68.27 ± 4.28	<0.001	68.47 ± 4.28	<0.001	68.22 ± 4.27	<0.001
	Body mass	−0.61 ± 1.37	0.655	−0.61 ± 1.37	0.567	−0.57 ± 1.36	0.675
	Urbanization	−0.70 ± 2.79	0.809	−2.14 ± 3.13	0.515	−0.64 ± 4.06	0.879

CHAPTER VII

Summary and general conclusions

During my thesis I studied some of the population and individual level effects of urbanization on a well-known synanthropic bird species, the house sparrow. In this final chapter I briefly summarize the main findings and conclusions, I overview some of the possible causes of the species' recent population loss and also suggest some directions for possible future studies.

In *Chapter III* I investigated the prediction that urban life may be more stressful for adult birds, reflected by their body condition (Shochat 2004), thus might be one of the reasons responsible for the smaller size of urban sparrows (Liker *et al.* 2008). This hypothesis was not confirmed by our results, as we did not find urban individuals to be leaner only to be proportionally smaller (when body mass was controlled to body size) compared to their rural conspecifics, and neither haematological or hormonal nor plumage traits we studied showed consistent habitat-related differences. Taken together, these condition indices do not indicate more urbanized environments to be more stressful for adult house sparrows.

In Chapter IV I studied the population trend of the house sparrow in Hungary based on census data and found a moderately declining population trend during the last decade. This chapter also investigated the urbanization-related differences in the species' breeding performance, both within the framework of field studies and experimental approaches. We showed that rural pairs fledge more (ca. by one fledgling) and larger (e.g. in body mass ca. 4 g) young per breeding attempt on average, and that these differences remained significant in both years of the study, despite the strikingly different weather conditions prevailing. The fact that rural and suburban broods did not differ in their average clutch size and hatching success suggested differences in the nestling development stage. This was also strengthened by habitat related differences in parental food deliveries and results of our two environmental manipulation experiments. This chapter raises a possible explanation that the lack of proper invertebrate food may be responsible for higher nestling mortality and hindered development in urbanized habitats, and also for the lower body mass found in urban sparrows.

In Chapter V I evoked the question whether predation pressure perceived by birds varies in relation to urbanization. We investigated this potential relationship in laboratory conditions by experimentally manipulating predation risk of house sparrows and measuring their risk taking behaviour. We showed that birds' fearfulness after simulated sparrowhawk attacks highly increased with age (from young to older birds) in urban but not in rural sparrows. Furthermore, comparing the older birds, urban sparrows responded more strongly to the predator attacks than rural birds. These results suggest that predation risk (at least posed by sparrowhawks) may be elevated in cities instead of being lower – which is contrary to the assumptions that urban areas are generally safer as urban bird populations are relaxed from top-down control (e.g. Shochat *et al.* 2006; Møller 2012).

Chapter VI validated a tool (based on the manual method of Liker *et al.* 2008 and the recent work of Czúni *et al.* 2012a) for a wide range of ecological studies which apply the urban-rural gradient approach to measure the degree of habitat urbanization. This semi-automated method objectively ranks differently urbanized habitats by using surface cover data from freely accessible aerial images. We showed that, when ranking differently urbanized habitats along an urban-rural gradient, our semi-automated method performs equally well compared to the manual method introduced by Liker *et al.* (2008) and to the more precise, polygon based surface classification conducted in ArcGIS. We also demonstrated that when replicating the analyses of ***Chapter III*** (using the same dataset), the application of the three urbanization-measuring methods lead to the same biological conclusions. However, the semi-automated method requires significantly less time than the other two approaches.

These results, that adult sparrows do not have lower body condition in cities, reaching lower reproductive success while are potentially exposed to higher predation risk (at least posed by sparrowhawks) compared to their rural conspecifics, are consistent with the relaxed 'bottom-up control' theory attributed to urban environments, and do not fit to the predictions of the 'credit-card hypothesis' (Shochat 2004). This latter model assumes resource overexploitation and also that mainly bottom-up regulation drives urban bird communities (via enhanced intra- and interspecific competition), eventually leading to high densities of urban individuals with generally inferior body condition. This latter assumption was not supported by our results. Furthermore, the findings of ***Chapter III*** and ***IV*** (the common garden experiment) also complement the former results of Bókony *et al.* (2010) who compared urban and rural sparrows and found neither condition dependency in their competitive performance nor reduced competitive ability in urban individuals. The 'credit card hypothesis' also assumes that, compared to wildlands, the relative importance of 'top-down control' (i.e. population regulation by predators) is altered in cities and suggests predation relaxation for avian prey populations, finally resulting in their higher densities. The results in ***Chapter V*** indicate higher perceived predation risk for adult birds in cities, at least posed by the sparrowhawk, which does not conform into the framework of Shochat's model.

At first glance, the smaller body mass of urban adults (see ***Chapter III*** and reported formerly by Liker *et al.* 2008) may also imply increased predation risk in cities, due to the theories of mass-dependent predation risk and strategic mass regulation of prey. Small birds are building up their fat reserves daily, the amount of which is assumed to reflect a trade-off between predatory and starvation risks. This trade-off arises because increased fat reserves promote an individual's survival probability (due to reduced starvation risk, especially under unpredictable conditions) while, on the other hand, greater fat load restricts manoeuvring abilities or hinders acceleration during an escape flight (Witter *et al.* 1994). Thus, this theory predicts that when perceived predation risk is high (and food predictability allows it), prey is expected to keep its fat reserves at lower levels (a trade-off between the risks of predation and starvation). This prediction has gained some support from both experimental (e.g. in great tit *Parus major;* Gentle & Gosler 2011) and correlative studies (e.g. in house sparrows; MacLeod *et al.* 2006). However, as in the study by Liker et al. (2008) both urban and rural adults lost significant weight during captivity and the mass difference between habitats persisted during the study the authors concluded that urban sparrows' smaller body mass was likely not the result of an easily reversible condition of strategic mass regulation. Instead, this finding and that of urban birds have smaller tarsi might refer to either morphological adaptation to high predation pressure (genetic adaptation; see Gosler *et al.* 1995) or to environmental stress during early nestling development, or both. However, findings of ***Chapter IV*** do not conform into this concept: results of both the common-garden and the nestling-swapping experiments underscore that environmental conditions during nestling development can be responsible for smaller body size, instead of inherent factors. Here, despite the lack of proof for genetic adaptation to strong predation and based on results of ***Chapter V***, we can speculate that predation risk by sparrowhawks may be increased for urban sparrows. However, we should be careful not to make broader generalizations on urban predation pressure by different predator species, as the findings of ***Chapter V*** tell us nothing about the predation by cats, for example. The role of cats as predators would be important to compare between habitats as cats are present all over the world with humans. Furthermore, they reach higher numbers than any native predator in urban areas, far above their natural carrying capacity, due to caring and subsidies provided by humans. Although their actual predatory role has been debated in the latest decade (i.e. they are causing only compensatory mortality by killing birds of poor condition), there is a growing body of evidence that they are very important predators in urban areas, (e.g. Baker *et al.* 2008; Dauphiné *et al.* 2009; Stracey 2011; Loss *et al.* 2013) especially for juvenile birds. A recent study from the USA (Loyd *et al.* 2013) that applied cat-borne video cameras to record pet cats' activity reported that only 23% of their prey items were carried home, implicating that previous studies based on cat owners' survey certainly and highly underestimated the actual predation rates posed by free-ranging cats. Whether this proportion is only the 'doomed surplus' of prey populations (i.e. individuals that would have died anyway e.g. from age or parasites) or cat-posed mortality significantly contributes to population loss, is still an open question. The sublethal effects of domestic cats to birds was also gained empricical support recently, as in their current study Bonnington *et al.* (2013) showed that the mere presence of cats around nests resulted in reduced parental provisioning rates and increased chance of nest predation – the latter due to the conspicouos nest defence behaviour of parents. That in ***Chapter V*** we failed to evoke antipredator responses from birds in the cat test is presumably due to shortcomings in the applied experimental design. Since it is known that both speed and direction of a predator's approach increases the level of threat perceived by the prey (Stankowich & Blumstein 2005), my future intent is to repeat the experiment with a more proper simulation of a cat attack. Additionally, it would be also interesting to measure the antipredator responses of sparrows, but this time being housed in small flocks, not solitarily. The logic behind this is that in nature, house sparrows are highly social during most of their activities (e.g. when encountering predators), thus it is reasonable to expect that they behave more 'naturally' in the presence of their conspecifics compared to the situations when they are separated from them.

Despite its historical success as a human commensalist, the house sparrow has been declining since the early 1980s at many parts across the Earth (see ***Chapter I*** and references in it). From the UK's long-time monitoring schemes we know that population decline is more severe and started somewhat later in urban areas compared to farmland regions (Summers-Smith 2003). In Hungary, the regional trend of the house sparrow also shows depression in the last decade, similarly to many parts of the species' range, but we still do not know the finer scale spatial patterns of this population loss. Thus, further studies are needed to test whether local population trends are related to the intensity of habitat urbanization in Hungary.

At the present, there are a number of different putative reasons suggested to lie behind urban sparrows' recent population declines, yet our understanding on this topic isn't satisfactory. In the following paragraphs I will discuss briefly some of the possible explanations which are related to the research presented in this thesis.

First, changes in predation-related mortality are amongst of the most self-explanatory reasons to start with when perceiving depression of prey populations. The above paragraphs of this Chapter already discussed the debated role of cats, domestic and feral, in terms of songbird mortality. Of course, besides cats there are other significant predators that may play important role in this question, i.e. the sparrowhawk. Despite the facts that the sparrowhawk is noted as the cardinal predator of many small songbird species (especially of juvenile individuals) and that its numbers increased to 170% during 1975-1990s in Britain (Baillie *et al.* 2009), its role in songbirds' population decrease has been generally considered to be unimportant (e.g. Newton 1997). According to this surmise, a national scale study in England, focusing on correlations between several predator (both avian and mammal) and prey species' densities (including the house sparrow) found very few negative correlations, some of them being biologically unlikely (Newson 2010). Contrary to this, a recent study (Bell *et al.* 2010) also from Britain, argues that decline in sparrow populations can be attributed chiefly to the increased predation by sparrowhawks due to the raptor's recovery and continuous spread after the DDT era. This latter study is convincing, as it points out that the start of urban sparrow populations' decline is fairly coincident with the resurgence of sparrowhawk populations and their colonization of urban habitats. Moreover, the variation in the timing of sparrowhawk's re-colonization of Britain also fits with the difference between the beginning of farmland and urban house sparrow population declines. Thus, the role of urbanizing sparrowhawks in sparrow population decrease should not be dismissed, especially as more and more studies report growing numbers of various raptor species breeding in urban areas (see the references in ***Chapter V***). In Hungary, last decade's census data on sparrowhawk indicates a regionally stable population both in breeding and wintering time (http://www.mmm.mme.hu/charts/trends), although we do not know the species' finer-scale spatial population dynamics, neither its relationship to the house sparrow's population dynamics. However, our method to quantify the degree of habitat urbanization (described in ***Chapter VI***) could also be used for detecting urbanization-related spatial changes in population trends not only in the case of the house sparrow but also for the sparrowhawk. As a subsequent step it would be interesting to see the last decade's parallel changes in the local numbers of sparrowhawk and house sparrow, in relation to urbanization, to explore any further similarities between the situation of Hungary and Britain. Such detailed, habitat-specific studies could help us to identify the potential associations of spatial dynamics of predator and prey species, not only at regional but at fine-scale level including different habitats. It is also important to note that while such correlative studies I cited in this paragraph are quite useful to identify links between trends and populations, they lack the potential to reveal causation, thus experiments are also needed to strengthen any relationships we may find.

Second, a further primary factor supposed to be responsible for the house sparrow's recent and severe urban decline is food shortage (e.g. Vincent 2005). As a result of abundant and predictable food sources in urban areas acquiring food may not be problem for adults, whose diet consists mainly of seeds and scraps. However, nestlings are strongly dependent of animal food during their first weeks of life, thus a shortage of invertebrate prey can critically limit their viability and development. While available quantitative data on densities of many arthropod taxa are poor, the elevated levels of pollutants, the higher proportion of pavement cover, the increased usage of pesticides in residential gardens and park areas, the strong thinning of shrub layer, mown turf and the removal of leaf litter in green spaces, and the reduced overall amount of vegetation (containing high proportions of exotic plants) are all assumed to reduce high density and diversity of arthropod species in urban areas. In line with this assumption, the results of ***Chapter IV*** showed that, opposed to adults, urban sparrow nestlings exhibit signs of habitat-related stress, as we found reduced survival rates and slower development in the more urbanized habitat, probably as an outcome of inadequate nestling food. Such conclusions, based on some correlational evidence, were also drawn by a study conducted in England (Peach *et al.* 2008), suggesting that some effects of urbanization might be similar in different parts of the species' range. These studies highlight that the reduction of arthropod food sources for birds and other insectivorous animals may be a general problem in urban habitats, which deserves further research.

Third, socioeconomic changes of urban habitats may also play important role in the species' population dynamics as sparrows seem to remain more prevalent in areas with only moderate changes in habitat structure and low socioeconomic status (Shaw *et al.* 2008). As a part of this the loss of suitable nesting sites is also connected to the continuous development and modernization of urban areas. Habitat alteration, such as the loss and improvement of weedy areas into highly maintained lawns also reduces foraging opportunities for both adults and nestlings, while modern, recently erected buildings usually lack suitable nesting opportunities, hampering the formation of loose breeding colonies this species would require. In built-up areas house sparrows typically prefer holes in the wall or crevices under the roof and their access to such nesting sites is strongly limited in modern or renovated buildings. There are several studies supporting the importance of these factors. In Britain, a national survey concluded that house sparrows prefer older buildings for nesting or newer ones with no roof repairs (Wotton *et al.* 2002). Similarly, a study from Chicago (Loss *et al.* 2009) showed that median housing age was strongly correlated with abundance of several bird species, including house sparrows, and also that lower per capita income of residents (possibly meaning more undeveloped patches) was a good predictor of high species richness and presence of many native bird species. Such a case was also reported from India (Singh *et al.* 2013), where the authors found strong positive correlation between numbers of mud houses and sparrow nests on them, and negative relationship between nests and concrete buildings, as during urban development mud houses has been substituted with more modern constructs. Other studies from Britain (Chamberlain *et al.* 2007) and Spain (Murgui 2009) emphasize the role of green patches (e.g. private gardens and small sized parks) as sparrows found to be present at higher densities in the proximities of these greeneries. These findings suggest that maintaining such areas may play key role in conserving the species.

However, it is important to keep in mind that the ‘urban matrix’ is a complex habitat, consisting of mosaics of different microhabitats, and built-up areas in cities are highly different across many parts of the globe. Thus, it is plausible that the relative importance of the above factors is region-specific. Although there are debates and speculations over the causes of decreasing sparrow numbers and despite the fact that several of the above putative explanations have been intensively studied (especially in Britain), the overall answer for the species’ population decline is still has to be waited for. It is also presumable that not a single overall factor, but a combination of them is responsible for the recent decline of house sparrows’ urban populations. To identify and disentangle the differences of the species’ population trends in urban and rural habitats we need small-scaled and detailed studies from areas of more the better. The software presented in ***Chapter VI*** is suitable for quantifying the degree of habitat urbanization for a great number of areas from which we have bird census data (collected within the frame of the Hungarian Common Bird Monitoring Scheme, ‘MMM’). Such analyses should certainly help us to identify a possible coarse-grained heterogeneity in the species’ population dynamics. It would also help us to clarify the role that habitat urbanization might play in the species’ recent decline, hopefully providing some insights into the underlying causal factors. The need for finer-scaled studies on population trends of species like the house sparrow stands not only for its own sake: common sedentary birds are suitable indicator organisms that can warn us about undesired ecological changes occurring in our severely altered environment. One might easily ask: if such a ubiquitous, resilient and adaptive species as the house sparrow, co-habiting with humans for so long, is suffering such major declines, then what fate is awaiting for more sensitive and less conspicuous ones? We have to identify the causal mechanisms responsible for this phenomenon in order to prevent more severe population loss and to be able to maintain habitats that are suitable not only for house sparrows but for a range of organisms striving to persist in our ever-expanding urban areas.

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VIII – THESIS POINTS

1. By measuring multiple indices of body condition I found no evidence of any systematic, habitat-related differences in stress responses or body condition of house sparrows. These results suggest that urbanization is unlikely to have a general negative effect on adult sparrows' health state.

2. In the field, I found similar clutch size and hatching success but significantly higher fledging success in rural compared to suburban nests, and also found that rural nestlings reached significantly greater body mass and size before fledging.

3. I found that chick-feeding rates did not differed between suburban and rural nests; however, parents of the latter delivered significantly larger prey items to their nests. Thus, nestlings received less and/or lower quality food in the suburban study site.

4. I showed that, when swapped 1-3 days old hatchlings between the nests in the field, nestlings in rural nests tended to grow larger compared to those developing in suburban nests, irrespective of their hatching origin.

5. Breeding in aviaries, under identical conditions, urban and rural parents achieved similar fledging success, and their nestlings' body mass, wing- and tarsus length did not differed significantly. Also, urban and rural parents fed their nestlings at similar frequencies. The results of points 3-6 imply that rearing environment of nestlings plays a key role in both the differences in breeding success and adult sparrows' body size (see thesis point #1).

6. I demonstrated that in simulated sparrowhawk attacks the behavioral response (i.e. the latency to feed after the startle) of urban birds increased strongly with age (hence presumably with experience), but found no such pattern in rural birds. I found that in the older age group the urban individuals responded more strongly than rural individuals. These results indicate higher levels of predation risk in urban habitats, at least posed by sparrowhawks.

7. I validated a formerly introduced manual method (Liker *et al.* 2008) for quantifying habitat urbanization, and based on this manual scoring process, I also introduced and tested a semi-automated method using only landcover characteristics from freely available satellite imagery. As this semi-automated method is the most time efficient and performed comparably well to other methods, I propose it as a useful tool for ecological studies applying broad measurements of urbanization.

TÉZISPONTOK

1. Különböző mértékben urbanizált élőhelyekről származó felnőtt házi verebek esetében nem találtam konzisztens élőhelyi különbséget az általam mért, kondíciót jelző tulajdonságokban. Mindezen eredmények alapján nem valószínű, hogy az urbanizációnak általános negatív hatása volna a kifejlett házi verebek kondíciójára, egészségi állapotára.

2. Terepi vizsgálataim eredményei szerint a fészekaljanként kiröptetett fiókák száma jelentősen magasabb a vidéki, mint a szuburbán pároknál, annak ellenére, hogy az átlagos fészekaljméretben és a kelési sikerben nem találtam élőhelyi különbséget. Továbbá, a vidéki fiókák mind testméreteikben, mind testtömegükben lényegesen meghaladták azonos korú, szuburbán fajtársaikat.

3. Terepen gyűjtött etetési megfigyeléseim szerint a fiókánkénti etetésszámban nincs eltérés a vidéki és szuburbán párok között, ugyanakkor a vidéki szülők lényegesen többször vittek nagyméretű rovartáplálékot utódaiknak. Ez arra enged következtetni, hogy a szuburbán élőhely fiókái alacsonyabb minőségű és/vagy kisebb mennyiségű fiókakori táplálékon nevelkednek.

4. További terepi eredményeim szerint, az 1-3 napos korukban vidéki és szuburbán fészkek között kicserélt fiókák esetében a vidéken fejlődő fiókák nagyobb méretűre növekedtek, függetlenül attól, hogy eredetileg vidéki vagy szuburbán élőhelyen keltek-e ki a tojásból.

5. Fogságban, azonos körülmények között szaporodva a vidéki és városi élőhelyekről származó madarak közel azonos szaporodási sikert értek el, és fiókáik testmérete, valamint testtömege sem mutatott élőhelyi eltérést. A fészkelésbiológiai paraméterek mellett a szülők fiókaetetési gyakoriságában sem találtam eltérést. A 3-6. pontok összegzett eredményei arra engednek következtetni, hogy a fejlődési környezet meghatározó szerepet játszik a szaporodási sikerben mutatkozó különbségek kialakításában, továbbá felelős lehet a városi, kifejlett verebeknél tapasztalt kisebb testméretért (ld. 1-es pont).

6. Fogságban tartott egyedeket szimulált karvalytámadásoknak kitéve kimutattam, hogy a predációs kockázatra adott viselkedési válasz (azaz az ijesztés utáni táplálkozási latencia) a városi madarak esetében erősen növekedett a korral (így vélhetően a tapasztalattal), míg vidéki egyedeknél nem tapasztaltam ilyen összefüggést. Továbbá, az idősebb korcsoportú madarak esetében a városi madarak erősebb kockázatkerülő magatartást tanúsítottak, mint vidéki fajtársaik. Ezen eredmények arra engednek következtetni, hogy a házi verebek a városi élőhelyeken nagyobb, karvaly általi predációs kockázatnak vannak kitéve.

7. A korábban Liker és mtsai. (2008) által bevezetett élőhely-urbanizáció mérésére szolgáló, kézi módszert validáltam, továbbá bemutattam és teszteltem egy félautomata, urbanizáció becslésére szolgáló eljárást, mely a kézi módszer metodikáján alapul, és felszínborítottsági adatok alapján becsüli az urbanizáció mértékét. A kézi- és félautomata módszerekkel, valamint az ArcGIS programmal meghatározott urbanizációs értékeket egy azonos ökológiai vizsgálat keretei között alkalmazva demonstráltam, hogy a három módszer minőségileg egyező eredményeket ad. Mivel a félautomata módszer adta eredmények megegyeznek a más módszerekéivel, ám azoknál jóval kevésbé munka- és időigényes, így alkalmas módszernek találom olyan ökológiai típusú vizsgálatokhoz, melyekben az urbanizáció mértékének durvább felbontású mérése elegendő.

IX – PUBLICATIONS

1. Papers included in the dissertation:

Seress, G., Bókony, V., Heszberger, J. & Liker, A. (2011). Response to predation risk in urban and rural house sparrows. *Ethology,* 117: 896–907. [IF: 1.945]

Bókony, V., **Seress, G.**, Nagy, S., Lendvai, Á. Z. & Liker, A. (2012). Multiple indices of body condition reveal no negative effect of urbanization in adult house sparrows. *Landscape and Urban Planning,* 104: 75–84). [IF: 2.173]

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Seress, G., Lipovits, Á., Bókony, V. & Czúni, L. (2014). Quantifying the urban gradient: an easy method for broad measurements. *Landscape and Urban Planning (in review)*

2. Papers not included in the dissertation:

Seress, G., Szabó, K., Nagy, D., Liker, A. & Pénzes, Z. (2007). Extra-pair paternity of Tree Sparrow (Passer montanus) in a semi-urban population. *Tiscia,* 36: 17–21.

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Czúni, L., Lipovits, Á. & **Seress, G.** (2012). Képi adatok közvetlen elemzése térinformatikai alkalmazásokban – Az urbanizáció becslésének módja adatbányászati eszközökkel. *Az elmélet és gyakorlat találkozása a térinformatikában III. Térinformatikai konferencia és szakkiállítás, Debrecen 2012* (ISBN: 978-963-318-218-5).

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3. Oral and poster presentations

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Seress, G., Szabó, K., Nagy, D., Liker, A. & Pénzes, Z.: Extra-pair paternity of Tree Sparrow (Passer montanus) in a semi-urban population. Előadás: *10th Behavioural Ecology Meeting, „Cooperation in animal socities", Babeş Bolyai University, Cluj Napoca, Romania, 2009. 23-24 January, 2009.*

Seress, G., Bókony, V., Pipoly, I., & Liker, A.: Morphological and reproductive differences between house sparrows (Passer domesticus) in relation to urbanization. Poszter: *11th Student Conference on Conservation Science, University of Cambridge, Cambridge, England, 23-25 March, 2010.*

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Czúni, L., Lipovits, Á. & **Seress, G.**: Képi adatok közvetlen elemzése térinformatikai alkalmazásokban – Az urbanizáció becslésének módja adatbányászati eszközökkel. Térinformatikai konferencia és szakkiállítás, Előadás: *Debrecen, 2012, május 24-25.*

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Czúni, L., Lipovits, Á. & **Seress, G.**: Estimation of Urbanization Using Visual Features of Satellite Images. Előadás: *KÉPAF, 2013. január29-február 01.*

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