

THE EFFECTS OF URBANISATION ON THE DEMOGRAPHIC PROCESSES IN BIRD POPULATIONS

Ph.D. Thesis

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Kivonat (magyarul)

A városokban az emberi tevékenységek nagymértékben átalakítják a természetes környezetet, így az ott jelenlévő élőlények számos tulajdonságukban különbözhetnek a természetes területeken élő fajtársaiktól. Ezek a változások lehetnek például az alkalmazkodás jelei az eltérő környezeti feltételekhez, vagy a városi ökológiai kényszerek (pl. eltérő táplálékbázis) hatásai. Az urbanizált élőhelyeken gyakran nincsen elegendő, jó minőségű rovar táplálék (hernyó) az énekesmadarak fiókái számára, ami számos faj esetében csökkent szaporodási sikert eredményez, vagyis kisebb fészekalj méretet és a fiókák rosszabb túlélését a természetes területekhez képest.

Doktori munkám során azt vizsgáltam, hogy mindezek fényében, a városi és erdei széncinege (*Parus major*) populációk demográfiai paraméterei mennyiben térnek el egymástól, valamint milyen táplálékforrások állnak a felnőtt madarak rendelkezésére a városi területeken. Vizsgálataim során 1) összehasonlítottam erdei és városi széncinege-populációk éves költési sikerét; 2) összehasonlítottam adult madarak látszólagos, éves túlélési valószínűségét erdei és városi populációk közt; 3) nyomon követtem a városi madarak territórium használatát a fiókanevelés során; 4) felmértem a téli madáretetés mértékét a városi élőhelyeken.

Eredményeink alapján a városi széncinegék éves szaporodási sikere szignifikánsan kisebb, mint az erdei területeken élő fajtársaiké, közel fele annyi fiókát tudnak csak felnevelni egy évben. A másodköltések gyakoriságában nem találtam élőhelyi különbséget. Várakozásaimmal ellentétben, az adult madarak éves túlélésében nem találtam szisztematikus élőhelyi különbséget, a legmagasabb és legalacsonyabb túlélési valószínűséget is városi populációkban becsültem (Veszprém: ~0,57; Balatonfüred: ~0,4), míg az erdei populációkban becsült túlélés köztes értékeket mutatott az évek során (Szentgál erdő: ~0,47; Vilma-pusztá: ~0,45). A városokban a szülő madarak a fiókáinak való táplálékgyűjtés során preferálják a nagyméretű őshonos fákat az idegenhonos, örökzöldeket pedig kerülik. Továbbá kihasználják az emberek által nyújtott táplálékforrásokat is, különösen a madáretetőket. Utolsó vizsgálatomban pedig arra a következtetésre jutottam, hogy a madarak számára rendelkezésre álló téli táplálékforrások mennyisége szintén jelentősen különbözhet városok között, mivel a lakosok által ebben az időszakban kihelyezett madáretetők denzitásában jelentős különbségeket találtam (Veszprém: 60.1–206.1/km²; Budapest: 23.3–83.0/ km²).

Abstract (in English)

In urbanised areas, human activities transform the natural environment in many ways, causing the local wildlife to differ in several characteristics from their conspecifics living in natural areas. These differences can be, for example, signs of adaptation to changed environmental conditions of urban habitats or the effects of urban ecological constraints (e.g. altered food supplies). In cities, there is often a lack of high-quality insect food (like caterpillars) for passerines' nestlings, which, in the case of many species, results in reduced reproductive success, i.e. smaller clutch size and reduced survival of nestlings compared to natural breeding habitats.

During my doctoral studies, I investigated the demographic parameters of urban and forest great tit populations, as well as the food sources available to adult birds in urban areas during the breeding season and wintertime. In the course of my research, 1) I compared the annual breeding success of forest and urban great tit populations; 2) I compared the apparent annual survival probability of adult birds between forest and urban populations; 3) I mapped the territory use and vegetation preference of urban birds during the chick-rearing period; 4) I surveyed the winter bird feeders in various urban habitats.

I did not find any habitat differences in the frequency of double-brooding between urban and forest-breeding females. However, the annual reproductive success of urban great tits was significantly lower than that of their conspecifics living in natural habitats, specifically the urban birds can raise half as many nestlings per breeding season. Additionally, I did not find any systematic habitat differences in the annual survival of adult birds. I estimated the highest and lowest survival probabilities in urban populations (Veszprém: ~ 0.57 ; Balatonfüred: ~ 0.4), while the survival estimated in forest populations showed intermediate values between (Szentgál forest: ~ 0.47 ; Vilma-puszta: ~ 0.45) over the study years. In cities, parent birds prefer large native trees and avoid non-native, broadleaved species when foraging and gathering food for their nestlings but also frequently take advantage of human-provided food sources, such as bird feeders. Contrary to my expectations, in my final investigation, I concluded that the amount of winter food sources available for birds could also differ significantly between cities, as I found significant differences in the density of bird feeders placed by residents during winter field surveys (Veszprém: $60.1\text{--}206.1/\text{km}^2$; Budapest: $23.3\text{--}83.0/\text{km}^2$).

Résumé (en français)

Dans les zones urbanisées, la pression anthropique transforme considérablement les espaces, si bien que la faune locale qui y vit en vient à se différencier de ses homologues vivants dans les zones rurales. Ces différences peuvent être, par exemple, des traits d'adaptation à des conditions environnementales modifiées des habitats urbains ou des effets de contraintes écologiques urbaines. Dans les villes, il n'y a souvent pas assez d'insectes de haute qualité nutritionnelle (comme les chenilles) pour les oisillons de passereaux, ce qui, pour de nombreuses espèces, entraîne un succès reproducteur réduit, c'est-à-dire une taille de couvée plus petite et une survie réduite des oisillons par rapport aux habitats de zone rurale.

Au vu de ces possibles changements, au cours de mes études doctorales, j'ai étudié les paramètres démographiques des populations de mésanges charbonnières urbaines et forestières, ainsi que les sources de nourriture dont disposent les oiseaux adultes en milieu urbain. Au cours de mes recherches, 1) j'ai comparé le succès reproducteur annuel des populations forestières et urbaines de mésange charbonnière; 2) J'ai comparé la probabilité de survie annuelle apparente des oiseaux adultes entre les populations forestières et urbaines; 3) J'ai cartographié l'utilisation du territoire par les oiseaux urbains pendant la période d'élevage des jeunes; 4) J'ai étudié les mangeoires d'oiseaux d'hiver dans les habitats urbains.

D'après nos résultats, le succès reproducteur annuel des mésanges charbonnières urbaines est nettement inférieur à celui de leurs congénères vivant dans des habitats naturels. En effet, les oiseaux urbains peuvent élever deux fois moins d'oisillons par saison de reproduction par rapport aux oiseaux forestiers. De plus, je n'ai trouvé aucun effet du type d'habitat dans la fréquence des doubles couvées. Dans les villes, les oiseaux préfèrent les grands arbres indigènes et évitent les espèces à feuilles larges non indigènes lorsqu'ils rassemblent de la nourriture pour leurs oisillons. Tout en profitant également des sources de nourriture fournies par l'homme, comme les mangeoires pour oiseaux. Contrairement à mes attentes, je n'ai trouvé aucune différence systématique d'habitat dans la survie annuelle des oiseaux adultes. J'ai estimé la probabilité de survie la plus élevée et la plus faible dans les populations urbaines (Veszprém: ~0,57; Balatonfüred : ~0,4), tandis que la survie estimée dans les populations forestières montrait des valeurs intermédiaires entre (forêt de Szentgál : ~0,47 ; Vilma-pusztá: ~0,45) au cours des années étudiées. Dans mon étude finale, j'ai conclu que la quantité de sources de nourriture hivernale disponibles pour les oiseaux pouvait également différer considérablement entre les villes, car j'ai trouvé des différences significatives dans la densité des mangeoires pour oiseaux placées par les résidents lors des études de terrain hivernales (Veszprém: 60,1–206,1/km²; Budapest: 23,3-83,0/km²).

1. General introduction

1.1. Environmental and ecological effects of urbanisation

Cities cover only 3% of Earth's land surface, but urbanisation has become one of the most common causes of species endangerment (Maxwell et al., 2016). In the last decades, an increasing proportion of natural habitats were transformed into built-up areas, while the extension of the urban landcover doubled between 1985 and 2015 growing from 362,747 to 653,354 km² (Liu et al., 2020). In 2018, 55% of the world's human population lived in cities, while this number was even higher in high-income regions and countries, like Europe where 74.5%, and also in Hungary where 71.4% of the population lived in cities (United Nations Human Settlements Programme, 2022). As in many other post-socialist countries, in Hungary, suburbanisation is one of the most determinative processes of urban development. A typical case is when the population from the cities emigrates and settles in villages previously attached to cities and their associated agricultural areas and scattered settlements (Vasárus, 2022), thus these former (mostly) agricultural villages turn into suburban areas.

Urban and suburban areas differ from rural areas in several environmental aspects, due to the intense landscape-transformation and other human activities, and the patterns of these changes vary highly between cities, regions and continents. As a consequence of these altered environmental features, urban habitats have numerous ecological effects on organisms from the individual to the community level, which alter wild animal population dynamics and demography in cities. However, changes in certain environmental factors alter populations in different ways based on the species' needs, so the effect of urbanisation is not uniform through animal taxa. During the last three decades, in the field of urban ecology, several researchers investigated these complex, interesting, and significant processes in urban habitats.

Globally, cities are characterized by increased levels of air pollution. The use of internal combustion vehicles powered by petrol or diesel engines, industrial activities, and home stoves and fireplaces which use solid fuels such as wood, coal, and wood waste, release pollutants such as carbon monoxide, sulphur dioxide, and nitrogen oxides into the air (Chatelain et al., 2021; Cohen et al., 2004). Heavy metals, such as lead, cadmium or zinc, are mainly emitted by anthropogenic activities involving fossil fuel combustion thus are especially abundant in the atmosphere and soil along roads (Johnson & Munshi-South, 2017). These pollutants are particularly problematic for plants and animals due to their accumulative properties and persistent nature, especially for species in higher trophic levels, like apex

predators and scavengers (Ortiz-Santaliestra et al., 2015, 2019). Exposure to heavy metals and other pollutants with a cumulative impacts, like lead, nickel, or arsenic, can have numerous physiological and behavioural impacts on an organism. Based on the type, length, and intensity of the pollution, these detrimental effects (for example: poor growth and development, decreased motor function, testicular damage, bone decalcification, and much more) could also vary between species, sexes, and age groups (Murgui & Hedblom, 2017; Ortiz-Santaliestra et al., 2019). All around the globe, increased amounts of heavy metals were reported in the eggs of several species from several taxa in urban environment (Croteau et al., 2008), including common frog (*Rana temporaria*, Meland et al., 2013), common chameleon (*Chamaeleo chamaeleon*, Díaz-Paniagua et al., 2002), green sea turtle (*Chelonia mydas*, Frossard et al., 2020), rook (*Corvus frugilegus*, Orłowski et al., 2014) and great tits (*Parus major*, Chatelain et al., 2021; Hargitai et al., 2016).

Another characteristic environmental shift along the urban-rural gradient is the so-called heat island effect, i.e. the average annual temperature in cities is higher than in the surrounding rural areas (Deilami et al., 2018). One of the main reasons for this phenomenon, in addition to air pollution, is that the surface of cities is largely covered by artificial materials (Bartholy et al., 2013), such as concrete and asphalt, which absorb a large proportion of the sun's heat and reflect it back into the air (Grimmond, 2007). The urban heat island, combined with the effect of global warming leads to increased frequency and intensity of the extent of extreme heat waves in these areas (Debbage & Shepherd, 2015). The high cover of impermeable surfaces also contribute to the heat-island effect. Buildings and roads are also a major altering and defining characteristic in cities, but these built-up areas are unsuitable for many animal species as foraging or breeding sites (Kark et al., 2007; McKinney, 2008; Ramírez-Mejía et al., 2020). The high ratio of built-up areas means a low ratio of green spaces, and these latter areas are usually highly fragmented. This also means that the suitable habitats for several animal species in cities are also highly fragmented and the patches are usually not connected with green corridors (Aziz & Rasidi, 2014; Brehme et al., 2013). Thus, as former studies pointed out, urban habitats increase the strength of random genetic drift and restrict gene flow, due to the fragmented habitat structure there (Miles et al., 2019). Especially for species with low dispersal ability, fragmented habitats could isolate populations living in separate patches, and potentially obstruct gene flow between populations and increase genetic drift within populations (Delaney et al., 2010; Fusco et al., 2021; Hitchings & Beebee, 1997). Even taxa with good dispersal abilities such as mammal species and birds have shown some degree of genetic isolation between subpopulations in urban parks (Avilova et al., 2023; Björklund et al., 2010; Selonen et al., 2018). Birds and mammals actively disperse between

fragmented habitat patches along the rural-urban gradient, as former studies of these taxa did not find genetic isolation between urban and rural populations (Avilova et al., 2023; Björklund et al., 2010; Selonen et al., 2018; but see: Miles et al., 2019).

Urban green spaces are typically under intense management (e.g.: lawn mowing, tree pruning and collecting leaf-litter and other materials), which means that humans create variation in the density, diversity, and complexity of vegetation, and maintenance practices include pulsed inputs of fertilizers, water, and pesticides. These practices drastically affects vegetation's biomass and could decrease the abundance of food sources for some herbivore species (Kowarik & von der Lippe, 2018; Singh et al., 2018). Recent studies reported a decrease in insect diversity, abundance, and biomass in cities (Dale, 2018; Fenoglio et al., 2020). However, arthropods do not always show consistent responses to urbanisation, as some species reached their highest abundance at an intermediate level of urbanisation, suggesting a non-linear relationship (Korányi et al., 2025). In highly urbanised sites, fewer native and more generalist insect species were found compared to less densely built areas (Dale & Frank, 2014; Szabó et al., 2023). This shift indicates that a few generalist species are able to adapt well to urban environments and can reach significantly elevated population densities (Korányi et al., 2022). Additionally, habitat patch quality factors play an important role in shaping the diversity of specialist herbivores (Herrmann et al., 2012).

Still, the generally lower insect biomass in urban areas is expected to have cascading effects through food webs and impact higher trophic levels (Tallamy & Shriver, 2021), like passerines during their chick-rearing period. For example, the decreased biomass of caterpillars has a strong negative effect on great tits' breeding success (Seress et al., 2020), and this may force the parent birds to change their chick-feeding behaviour in urban habitats and utilize alternative food sources (Sinkovics et al., 2021). In some cases, tits start to prey on mites, scales, and adelgids, because these insect taxa are able to complete multiple generations on the same plant thus, potentially can increase their populations in urban habitats. The reason of this is that tree resistance to herbivores is typically decreased by fertilization (common management methods), which is common practice in city management (Raupp et al., 2010; Singh et al., 2018).

In addition to this, urban areas are highly affected by anthropogenic light and noise pollution (Wilby & Perry, 2006; Zannin et al., 2006). Furthermore, due to their pervasive nature, these pollutants disrupt ecological processes and alter auditory and visual behaviour of several species far beyond the directly affected areas (Ditmer et al., 2021; Kyba et al., 2011; Longcore & Rich, 2004). Exposure to noise and light pollution can also lead to changes in animals' physiology and behaviour. Prolonged light pollution affects animals' orientation,

migration, and circadian and seasonal hormonal rhythm (Dominoni et al., 2013; Longcore & Rich, 2004). It also affects the local animal communities, as strong light sources (for example street lamps) attract high amounts of nocturnal arthropods, which also attract their predators like frogs, nocturnal lizards, and bats (Degen et al., 2024; Eisenbeis & Hanel, 2009; Shimoda & Honda, 2013). Both light and noise pollution can affect the animal's communication (Da Silva et al., 2015; Smit et al., 2022). The latter especially affect songbirds and frogs during their mating period, when they use acoustic signals to express territorial and mating behaviour and increased environmental noise level could disturb their natural behaviour (Cardoso et al., 2020; Perry et al., 2008 but see: Forsburg et al., 2021).

Not just these types of “indirect” disturbances from human activities but humans’ presence itself also can directly affect animals and their behaviour. In cities, animals are usually habituated at some level to humans’ presence, thus showing increased tolerance towards them, compared to their counterparts in natural habitats (Liker, 2020; Vincze et al., 2021). This is probably the result of the fact that citizens tend to act neutral towards wild animals in urban areas and do not pose a threat to them (Liker, 2020; Rebolo-Ifran et al., 2015; Vincze et al., 2021). While animals seemingly adapted well to human-induced stressors, they can cause adverse physiological effects. For example, great tit, which is a widespread and successful urban adapter species, usually show increased stress-related traits (Caizergues et al., 2022; Senar et al., 2017), and chronically increased stress levels could have a negative effect on several physiological traits (Bailly et al., 2016; Salmón et al., 2016; but see: Isaksson et al., 2009), and can potentially result in decreased reproduction or survival.

Another prominent feature of human settlements is the availability of new, alternative food sources. Urban-adapted mammals and several bird species (like crows, parrots, and several granivorous or omnivorous species) can exploit anthropogenic food sources, like food waste or food provided in bird feeders (Newsome & van Eeden, 2017; Robb et al., 2008; Tryjanowski, Skórka, et al., 2015). These sources offer easily available, predictable, and energy-dense food for wild animals in human settlements, allowing them to achieve high population densities (Burt et al., 2021; Carpenter & Savage, 2021; Tryjanowski et al., 2018). The increased abundance of synanthropic species, like house mouse (*Mus musculus*) and feral pigeon (*Columba livia domestica*) provide excellent food sources for several carnivore species (Marchesini & Bussolini, 2016). Even buildings can “create” new types of feeding sites, because artificially covered, shiny, dark surfaces, like solar panels, glass buildings, or cars reflect horizontally polarized light. Therefore, these surfaces can attract aquatic insects in mass, which, in turn, attracts their predators. For example, in Hungary, it was reported, that

several bird species have visited the glass buildings on the riverside to collect the caddisflies that swarm on their glass panels (Pereszlényi et al., 2017).

In the case of birds, it is the bird feeders and birdbaths that have been a cause for concern, because large numbers of birds congregating in small areas, creating an ideal environment for a disease outbreak, as is thought to have happened in the case of the greenfinches (*Chloris chloris*) and goldfinches (*Carduelis carduelis*) in France and England (Chavatte et al., 2019; Hanmer et al., 2022). Nevertheless, recent field surveys and experiments did not find any proof that bird feeders would be a source of transmissible diseases or pathogens or increase the infection rates for birds (Bichet et al., 2020; Frątczak et al., 2021; Schaper et al., 2021). For several mammal species, high population densities and consequent frequent interactions between individuals could increase the transmissible diseases' prevalence (Bradley & Altizer, 2007; Rodewald & Gehrt, 2014). Diseases with high mortality rates can dramatically reduce the host density in urban populations (Albery et al., 2022; Rothenburger et al., 2017), but less harmful pathogens could reach high density and diversity in urban host populations, like tick-borne diseases in hedgehogs (Szekeres et al., 2016, 2019).

Besides diseases, other sources of mortality are also changed in the urban environment. Predator-prey dynamics is one of the most important regulating factors of animal populations. Numerous studies reported that the predator species of passerines and their hunting opportunities are different in cities, but this does not necessarily mean that the degree of overall predation pressure is significantly different from natural habitats (Chamberlain et al., 2009; Perry et al., 2008; Rodewald & Gehrt, 2014). Although cities usually have an increased number and density of potential nest predators, such as cats, rats, some mustelid species, or jays and corvids (Fischer et al., 2012; Sorace & Gustin, 2009), the survival of bird nests is usually higher in cities than in natural areas, indicating decreased predation pressure in these areas (Gering & Blair, 1999; Kurucz et al., 2021; Vincze et al., 2017). However, predation of eggs and nestlings and predation of fledglings and adult birds involve different predator species, thus predation pressure on juveniles and adults is not necessarily relaxed in cities. Several raptor species that prey on birds, successfully adapted to the urban environment (see below).

However, domestic cats (*Felis catus*) pose the most serious threat as predators to songbirds and other small vertebrates worldwide (Lepczyk et al., 2023; Trouwborst et al., 2020). From North America to Antarctica, free-ranging cats have been responsible for dozens of species extinctions, and continue to pose a major hazard to hundreds of vulnerable species (Doherty et al., 2016; Loss & Marra, 2017). The populations of domestic cats can reach extremely high densities in cities (for example 229 cats/km² in Bristol, UK; Baker et al.,

2005), and the resulting predation pressure posed by cats alone can reduce the survival probability, population size, and growth rate of small vertebrate populations (Baker et al., 2005; Bonnington et al., 2013; van Heezik et al., 2010). Predation on birds by cats is typically greatest in spring and summer, probably reflecting the killing of juvenile individuals (Baker et al., 2005). This substantial loss of fledglings can cause a significant decrease in the growth rate of these bird populations, thus threatening their self-sustainability (Bartos Smith et al., 2016).

Other than domestic cats, wildlife in cities has to face additional new types of dangers that they do not encounter in their natural environment (Chace & Walsh, 2006). For example, although American fox squirrels' (*Sciurus niger*) survival probabilities are very similar in rural and urban populations, in cities most squirrels were killed by vehicles, while in rural areas predation was the leading cause of death (McCleery et al., 2008). Vehicles can also take many victims among birds in cities, but this can be even greater along rural roads, where vehicles typically travel at higher speeds than in residential areas (Rodewald & Gehrt, 2014). Also, collision with windows is a very significant mortality factor in urban bird populations (Loss et al., 2015). On the other hand, buildings can provide dens and nesting sites for small- and medium-sized mammals (e.g. bats), birds, reptiles, and arthropods (French et al., 2018; McCleery, 2015; Murgui & Hedblom, 2017).

Despite the highly variable environmental changes between cities, regions, and continents, the species richness of the urban flora and fauna often decreases with intense urbanisation (Dallimer et al., 2012; McKinney, 2008), as it has been reported for various taxa such as plants (Ruas et al., 2022; Yan et al., 2019), arthropods (Piano et al., 2020), amphibians (Callaghan et al., 2021), reptiles (French et al., 2018), birds (Batáry et al., 2018) and mammals (Fidino et al., 2020). In every taxon, only those individuals (thereby species) can survive in cities that are able to adapt to this novel set of conditions (Crocì et al., 2008). Therefore, getting to know a species' demographic factors is crucial to understand how (if even) it could survive in urban environments.

1.2. Demographic changes in populations of urban animals

As I discussed above, due to the strongly modified environment in our cities, urban animals usually have altered behavioural, hormonal, and other physiological features. Moreover, the effects of urbanisation likely vary substantially across taxonomic groups due to differences in habitat requirements and life history characteristics. While for some vertebrate taxa (e.g. birds and mammals) we have a better understanding of these changes, unfortunately, we still do not know much about the effects of urbanisation on the reproductive success and survival of some other taxa, such as fishes (Marques et al., 2022), amphibians (Scheffers & Paszkowski, 2012) and reptiles (Brum et al., 2023). For example, the few former studies published so far showed mixed effects of urbanisation on frogs' and salamander species' reproduction (Hamer, 2022; Skidds et al., 2007) while in reptiles, the effect of urbanisation could vary between species based on their lifestyle. Semi-aquatic species, like turtles and water snakes, maintain and sometimes even increase their survival, and reproductive output in urban habitats (Eskew et al., 2010; Ferronato et al., 2017; Pattishall & Cundall, 2009). However, as French et al. (2018) pointed out in their review, urbanisation usually leads to a decline in population size and an increase in mortality rates in terrestrial reptile populations (Endriss et al., 2007; Knapp & Perez-Heydrich, 2012).

Compared to other animal taxa, mammals and birds are generally well studied. Still, researchers have started to study more intensively these taxa populations' demography in urban habitats only during the last decade (Sepp et al., 2018). These studies found that, generally speaking, omnivores, generalists, and medium-sized carnivore species are more likely to colonize the cities and be able to utilize the new resources there (McCleery, 2015). It has also been showed that many urban adapted mammal populations have increased their reproductive success (Santini et al., 2019) compared to their rural counterparts, as their females produce larger litters, like black bears (*Ursus americanus*, Beckmann & Berger, 2003) and red foxes (*Vulpes vulpes*, Bateman & Fleming, 2012) or reproduce more often, like island foxes (*Urocyon littoralis*, Gould & Andelt, 2011) and fox squirrels (*Sciurus niger*, McCleery, 2009).

Typically, urban-adapted mammal populations show increased survival probabilities and better body condition in cities (Bateman & Fleming, 2012; McCleery, 2015). This is particularly important because adult survival could have a stronger influence on populations' growth rate (λ) than adults' fecundity, as was the case of the urban maternity colonies of big brown bats (*Eptesicus fuscus*) in Fort Collins (O'Shea et al., 2011). The increased body condition, fecundity, and survival of urban mammals at least partly resulted from the increased amount of food available in cities, which many species have learned to use

efficiently (discussed above). However, in some cases, urbanisation does not necessarily affect the survival rates but alters the mortality causes. College Station (Texas, USA) fox squirrels died in 60% of cases due to vehicle collisions, while predation was the cause of mortality in 60% of cases in nearby rural populations (McCleery et al., 2008). A drastic shift like this, from predation to anthropogenic causes, could mean a new kind of selection pressure to which the urban animal must adapt.

When considering birds, raptors may be more sensitive to urbanisation than other avian taxa, as large-bodied raptors such as eagles are generally absent or rare in urban areas, most likely because of their larger home range sizes and specific habitat requirements, or diets on small mammals and animal carcasses (Chace & Walsh, 2006; Kettel et al., 2018; Mannan & Steidl, 2018). However, several raptor species colonize and exploit urbanised areas as breeding habitats around the globe, particularly medium-sized species that are specialized on avian prey (Mannan & Steidl, 2018) such as hawks (Millsap, 2018), falcons (Kettel et al., 2018) and some owls (Millsap & Bear, 2000). In some cases, these species can reach similar, like black sparrowhawks (*Accipiter melanoleucus*) in Cape Town (Sumasgutner et al., 2019), or even higher reproductive success in urban than natural habitats, like Cooper's Hawks (*Accipiter cooperii*) in Wisconsin (Rosenfield et al., 2019) or peregrine falcons (*Falco peregrinus*) in Great Britain (Kettel et al., 2019), mainly as a result of increased amounts of avian prey and decreased nest predation rate (Sarasola et al., 2018).

Urban songbirds typically start breeding seasonally earlier and often have decreased reproductive success, such as lower clutch size, chick weight, and fledging success compared to their conspecifics living in more natural habitats. Several species tend to fledge fewer offspring per brood in urban habitats, for example, house wrens (*Troglodytes aedon*; Grabarczyk et al., 2022), collared and pied flycatchers (*Ficedula albicollis* and *F. hypoleuca*; Vaugoyeau et al., 2016), house sparrows (*Passer domesticus*; Seress et al., 2012), great tits (*Parus major*; Biard et al., 2017; Seress et al., 2018), blue tits (*Cyanistes caeruleus*; Gładalski et al., 2016) and barn swallows (*Hirundo rustica*; Teglhøj, 2017). There are also examples of the opposite (i.e. higher success in cities), as in the case of the northern mockingbird (*Mimus polyglottos*; Stracey & Robinson, 2012). However, it is important to note that former studies typically examined only the success of the first nesting attempts during the breeding season, even though most of the investigated species are typically facultative double-breeders (Del Hoyo et al., 2007). However, not taking into account the success of the second clutches could lead to biased results about the overall reproductive success, as multiple breeding per season could be an effective strategy to raise reproductive success (Cornell & Williams, 2016; Hoffmann et al., 2015).

While the reproductive success of many avian species along the urban-rural gradient has been studied relatively well (Chamberlain et al., 2009), the patterns in survival rates in relation to habitat urbanisation have been explored for far fewer species. Consequently, even fewer studies have described the rate of population change in urban bird populations or could compare these between populations in urban and non-urban habitats (Sepp et al., 2018). Despite this lack of information, the changes in populations' survival rates and demography are probably still the most studied in birds compared to other taxa in urban environments. A good example of this is the study by Kauffman et al. (2003), which used more than two decades of data (between 1977 and 1999) on the urban and rural populations of American peregrine falcons (*Falco peregrinus anatum*) and could model the falcon populations' different demographic parameters, like fecundity rates and survival rates, at different life stages. This unique, long-term dataset revealed, that American peregrine falcons in urban habitats have significantly higher fecundity rates and survival than birds in rural habitats and that the temporally averaged population growth rate in urban habitats was estimated as $\lambda=1.28$ (growing), compared to $\lambda=0.99$ (stagnant) in rural habitats (Kauffman et al., 2003). Interestingly, the temporal analysis revealed, that while the yearly estimates of λ values predicted declining population growth in rural habitats in the first decade, this changed in the second decade, as the estimated λ showed increasing population trends, due to increased reproductive success. This improvement in the rural populations' reproductive success was attributed to the intensive reintroduction program and species conservation efforts between 1977 and 1992. The authors of this study concluded, that the increased population growth rate in cities could be the result of the general lack of natural (nest) predators, the abundant prey base of Rock Doves (*Columba livia*) and other avian prey species, and the availability of suitable nesting sites in the form of skyscrapers and bridges in cities. Similarly, but for a different raptor species (Cooper's Hawks) in Albuquerque, a growing population trend ($\lambda=1.29$) was reported for an urban population (Millsap, 2018). There, adult survival was the most important accounting factor for the annual variation in λ , and regarding the putative drivers, the authors hypothesized that while rural populations suffered from an increased mortality rate due to increased exposure to DDT, urban hawks benefited from the high abundance of winter prey present in cities.

Unlike raptors, for small, passerine species, urban areas sometimes do not provide a safer environment. For example, when scientists estimated the growth rate of breeding populations of spotted towhees (*Pipilo maculatus*) in urban parks of Portland, their results showed that only 2 out of 4 were self-sustaining (Bartos Smith et al., 2016), even though there were no differences between parks in adult survival, only in breeding success. The decrease in the

breeding success in the two parks was probably the result of the increased predation pressure by domestic cats. Logically, population demography factors could highly differ between even the urban-adapted passerine species (Evans et al., 2015) and population demography models show a concerning picture of the effect of urbanisation in the case of other species, like blue tits (Eden, 2021). Few studies have compared the demographics of urban and rural populations, largely due to the need for long-term, detailed data to estimate parameters like annual survival. Yet such data are essential to understand how urbanisation affects species over time. It's also crucial to identify the traits that enable certain species, populations, or individuals to thrive in urban settings—and, perhaps more importantly, to determine what types of urban environments allow wildlife to survive and coexist with humans.

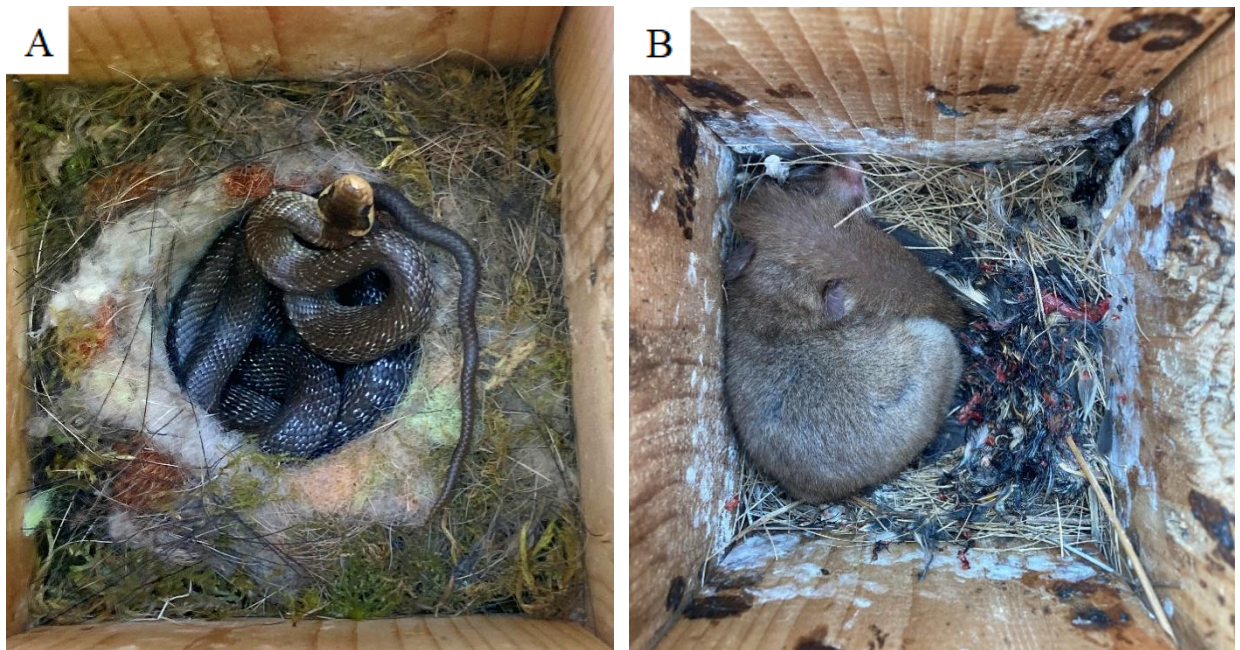


Figure 1.1. (A) Aesculapian snake (*Zamenis longissimus*) and (B) european edible dormouse (*Glis glis*) in passerines' nest, within nestboxes. These two species are the most common nest predators in our forest study sites and unlike the common nest predators in urban sites, like woodpeckers (*Dendrocopos* spp.) and eurasian jay (*Garrulus glandarius*), they usually prey the whole brood, often including the female parent on the nest (photos by Boglárka Bukor).

1.3. Thesis objectives

In my doctoral studies, my general aim was to investigate the effect of urbanisation on the demographic parameters of urban birds. First, I estimated and compared the annual breeding success of two urban and two rural breeding populations of great tits (see more: Chapter 2. General field methods). Second, I estimated and compared the annual survival probabilities of adult great tits in two urban and two rural breeding populations. Third, because former studies conducted in the same study system already found evidence that the major limitation factor of urban great tits' breeding success is the poorer food supply for chicks, I investigated how the foraging patterns, habitat, and vegetation use of great tit parents are affected by the vegetation composition in urban green areas during the breeding season. Fourth and finally, I surveyed the available anthropogenic winter food supplies for birds in two cities, because this factor could have a major influence on birds' annual survival.

Specifically, I had the following research objectives:

Objective 1: To compare the frequency of double-brooding great tit females and the number of their annually fledged chicks in two urban and two forest habitats.

Objective 2: To compare the annual survival probabilities of adult great tits, between two urban and two forest breeding populations, and to test the effect of various factors (age, sex, and study year) on birds' survival.

Objective 3: Study the habitat use of urban breeding birds in Veszprém during the chick-rearing period by combining radio-telemetry tracking, real-time observations of birds' foraging behaviour, detailed plant surveys, and video recordings of nestlings' diet.

Objective 4: Survey the densities of winter bird feeders in two cities (Veszprém and Budapest) with respect to the feeder type, the food types presented in feeders, and the abundance and species richness of birds visiting the feeders.

These studies were carried out by the HUN–REN–PE Evolutionary Ecology Research Group at the University of Pannonia. I participated in all aspects of data collection and also had the opportunity to analyse the long-term and uniquely detailed dataset on great tits' breeding success and survival, in order to estimate these two key population demographic parameters.

2. General field methods

2.1. Study species

The great tit is a well-known species of urban ecology studies and this is the model species of my PhD thesis too (Figure 2.1.). This small bird belongs to the avian order Passeriformes and the family *Paridae*, has a wide distribution across Eurasia, from the British Islands to the river Amur. The great tit occupies a wide range of habitats, from natural woodlands, mixed forests, and forest edges to various human-transformed areas like gardens, urban public parks, and farmlands. In Hungary, the great tits' population show a moderately growing trend since 1999 (Szép et al., 2022). The species is resident there, or partially and temporally migrant in harsh winters. The post-fledging dispersal is also typical, but usually short distance, around ~2-3 km (Könczey et al., 1997). The great tit is predominantly insectivorous, but in the winter, it also consumes a broad range of seeds and other plant materials, and it also frequently visits winter bird feeders in human settlements.

The great tit nests in almost any form of cavities, crevices or in urbanised habitats almost any closed space or hollow (e.g. post boxes, fence pipes) and also readily accepts artificial nest boxes (Figure 2.2.). Although the great tit is socially monogamous, extra-pair copulations occur regularly, and more frequently in our urban than rural study populations (Pipoly et al., 2019). Females lay one egg per day and incubate them for approx. 14 days. Males do not participate in the incubation of eggs. After hatching, both parents participate in the feeding of the nestlings who stay in the nest for 20 to 22 days (Haraszthy, 2019). After fledging, parents lead and feed their offsprings until they become independent (Haraszthy, 2019). Usually, the male parents do the majority of the post-fledging care, especially when the pair (facultatively) start a second brood after the first one (Verhulst & Hut, 1996). Then, the female starts laying or even incubating the eggs of the second clutch, while the male still guides the fledglings from the first clutch (Verhulst, 1998). Adult great tits usually show strong breeding site fidelity and just rarely change territory between (or within) a breeding season (Andreaeu and Barba 2006).

Great tits successfully colonised the urbanised habitats and several former studies considered it as urban adapter species due to their common appearance in cities all over the temperate zone (Del Hoyo et al., 2007). This species has many of the typical traits of a successful urban adapter species like sedentary, omnivorous, widely distributed, cavity nester with a short lifespan (Kinnunen 2021) and successfully habituated to strong human disturbance (Vincze et al., 2021).



Figure 2.1. Adult female (left) and male (right) great tits (photo by Boglárka Bukor).



Figure 2.2. Nest box design in our study sites.

We attached a black plastic box for camouflaging the camera that we use to record parent birds' behaviour during chick-rearing. In the photo, a colour-ringed great tit parent just arrived with food for the nestlings (photo by Csenge Sinkovics).

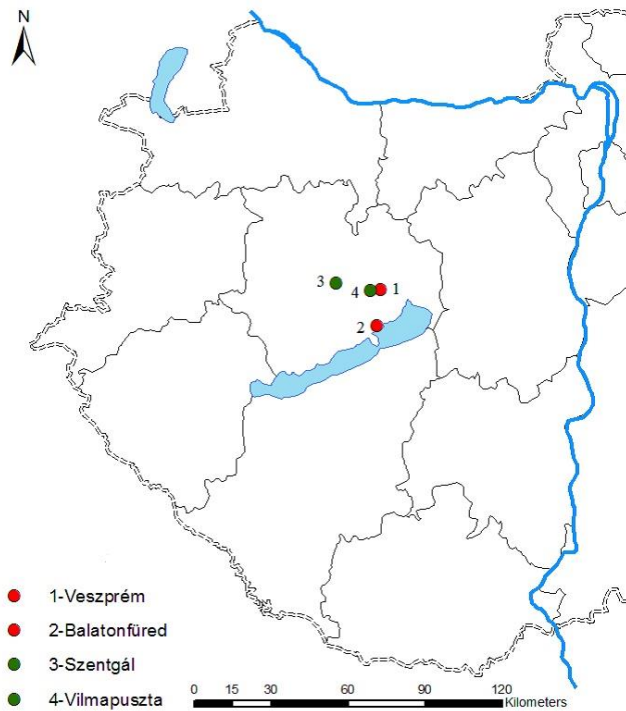


Figure 2.3. The map of our four study sites in Central Hungary (for studies in chapters 3-5), where the spots are indicating the urban (red) and forest (green) study sites.

2.2. Study sites (for studies in chapters 3-5)

We studied great tits breeding in nest boxes at two urban and two forest sites in Hungary from 2013 to 2021 (Figure 2.3.). In one of the urban study sites, Veszprém (47°05'17.29"N, 17°54'29.66"E), the nest boxes were placed in public parks, a cemetery, and a bus station, where human activity, vehicle traffic, and noise pollution are typically intense. At this site, Norway maple (*Acer platanoides*) and European ash (*Fraxinus excelsior*) are the most common native tree species, and horse chestnut (*Aesculus hippocastanum*) and black pine (*Pinus nigra*) are the most common non-native species. The average daily temperature (mean $\pm$ standard deviation [SD]) during the breeding season (March 1 – July 15) was 15.3 ± 1.85 °C (our unpublished data).

In the other urban study site, Balatonfüred (46°57'30"N, 17°53'34"E), the nest boxes were placed in a park (ca. 9 ha) in the central part of the city, which is surrounded by an urban matrix with residential areas and roads with heavy traffic. The small-leaved lime (*Tilia cordata*), the Norway maple, and the sessile oak (*Quercus petraea*) are the most common native tree species and the black pine is the dominant non-native species. Balatonfüred has a somewhat warmer climate than Veszprém and the two forest study sites: the average daily temperature during the breeding season was 16.4 ± 1.19 °C. Our monitoring work in Balatonfüred was finished in 2019 due to logistic constraints.

The two forest sites were located in mature woodlands near Szentgál (47°06'39"N, 17°41'17"E) and at Vilma-puszta (47°05'06.7"N, 17°51'51.4"E), 2-3 km away from the nearest human settlement. Szentgál is a mixed beech (*Fagus sylvatica*) and hornbeam (*Carpinus betulus*) forest. The average daily temperature during the breeding season was 13.4 ± 1.51 °C. Human activity is relatively rare in the study area, although there is regular logging and hunting during some periods of the year. Vilma-puszta is a mature deciduous woodland characterized mainly by downy oak (*Quercus cerris*) and South European flowering ash (*Fraxinus ornus*). The average daily temperature during the breeding season was 14.8 ± 1.47 °C. Vilma-puszta is a Natura 2000 site that is relatively free from human disturbance: it has no paved roads, there is only one nearby farm, and there is no logging activity; though it is occasionally visited by hunters and hikers. Both the Szentgál and Vilma-puszta sites represent common types of forests typical in Hungary (Borhidi A., 2003).

2.3. General fieldwork

We monitored the breeding of great tits in the artificial nest boxes by a standard protocol that we followed throughout the whole study period in all sites. We checked the nest boxes every 3 or 4 days from March to early July to record laying and hatching dates as well as the number of eggs and nestlings. When we found more than one egg during the first nest check, we back-calculated the first egg date by assuming that one egg was laid per day. We typically ringed each nestling at day 14-16 post-hatch (i.e. a few days before fledging; hatching day of the first chick = day 1) with a numbered metal ring, except in 2013 and 2014 when nestlings were also marked individually by three plastic colour rings.

We captured most parent great tits in their nest box during brood-rearing (typically at least 7 days after hatching) and marked each bird with a unique combination of one metal and three plastic colour rings. A smaller number of adults was caught during the winter at feeder sites with mist nets. Upon capturing, we determined the birds' sex and age based on their plumage characteristics and distinguished two age classes (Svensson et al., 2009): 1st-year birds (hatched in the previous breeding season; FY, EURING age code 5) and after first-year (AFY) birds (having at least one breeding season before the current one, EURING age code 6). We refer to both AFY and FY birds as adults in the rest of the thesis. Nest boxes were equipped with a non-transparent plastic box that served as concealment for a small video camera (see the detailed description in Seress et al. 2018). We video-recorded nests during the brood-rearing period and used 1 hours long videos to individually identify colour-ringed parents (ringed in earlier years). The same standard protocol for checking nests and catching, measuring, and marking birds has been followed at all study sites since 2012. Data collected in the field are entered into a systematic, verified database. Later, the database was used to extract the data needed for statistical analyses.

3. Double-brooding and annual breeding success of great tit in urban and forest habitats

Boglárka Bukor, Gábor Seress, Ivett Pipoly, Krisztina Sándor, Csenge Sinkovics, Ernő Vincze, András Liker

This chapter is an extended version of the research article “Boglárka Bukor; Gábor Seress; Ivett Pipoly; Krisztina Sándor; Csenge Sinkovics; Ernő Vincze; András Liker (2021) Double-brooding and annual breeding success of great tits in urban and forest habitats. Current Zoology, 2021 1-9.”

Introduction

Although dozens of studies compared breeding success between urban and non-urban populations (reviewed by Chamberlain et al., 2009; Sepp et al., 2018), these typically focused only on seasonally first broods even in species that are known to have second broods frequently (Reale & Blair, 2005). Having multiple broods per breeding season is a widespread strategy in birds to increase their annual reproductive success (Cornell & Williams, 2016; Hoffmann et al., 2015; L. Naef-Daenzer et al., 2011). Moreover, several features of urban habitats may facilitate this strategy. For example, the advanced leaf emergence of urban plants (Neil & Wu, 2006) can advance spring food availability, hence may result in seasonally earlier egg-laying in urban birds (Deviche & Davies, 2014; Seress et al., 2018, but see: Bailly, Scheifler, Berthe, et al., 2016), which in turn may increase the propensity of individuals to initiate seasonally second broods (Batey, 2018; Jackson & Cresswell, 2017). In non-migratory passerines, the abundant human-provided winter food sources (e.g. bird feeders) and the generally milder winter climate in cities might also result in better post-winter body condition, potentially helping females to lay earlier and produce multiple clutches within a breeding season (Galbraith et al., 2015; Gładalski et al., 2016; Pigeault et al., 2020; Verhulst, 1998). Consequently, the higher frequency of multiple broods per year may potentially compensate urban birds for their lower breeding success per breeding attempt or may even result in equivalent or higher annual reproductive output compared to their non-urban conspecifics (Muller et al., 2020; Reale & Blair, 2005).

Despite that, the frequency of double-brooding has important consequences both at the individual (lifetime reproductive success) and the population (population dynamics) level,

studies that compared the number of breeding attempts per year between urban and rural bird populations, are rare and their findings are equivocal. Some of the few studies that included multiple broods per female within a year found either no difference in the number of nesting attempts between urban and rural habitats (Batten, 1973; Leston & Rodewald, 2006; Luniak et al., 1992) or reported fewer (Luniak, 1992; Rodewald & Shustack, 2008) or a higher number of second clutches in cities (Cowie & Hinsley, 1987). Accordingly, urbanisation could affect the breeding habitat's features and so the probability of double-brooding in several positive and negative ways. To get a better understanding of the actual difference between urban and non-urban birds' reproductive success, we clearly need more information on how urbanisation affects the frequency of double-brooding and the number of fledglings produced during the whole breeding season.

To fill this knowledge gap, here we analysed breeding success data of a facultative double-breeder species, the great tit (Del Hoyo et al., 2007). Several former studies showed the negative effects of habitat urbanisation on great tits' clutch size (Caizergues et al., 2018; Seress et al., 2018; Wawrzyniak et al., 2015), hatching success (Bailly., 2016; Charmantier et al., 2017), body condition and nestling survival (Bailly et al., 2016; Corsini et al., 2020; Seress et al., 2020). In this study, we investigated two urban and two forest populations over the course of seven years and compared (1) the probability of double-brooding and (2) the number of annually produced fledglings per female between urban and forest habitats. Based on the earlier start of breeding in urban areas (Seress et al., 2018), we predicted a higher probability of double-brooding in urban versus forest habitats, and therefore a smaller between-habitat difference in the number of annually fledged offspring per female than when we consider only the seasonally first broods.

Methods

Study sites and Breeding Biology

We studied great tits breeding in nest boxes at two urban (Veszprém, Balatonfüred) and two forest sites (Szentgál, Vilma-puszta) in Hungary from 2013 to 2019. You can find a more detailed description of the study sites in chapter 2.2. *Study sites*.

In total, there were 315 to 353 nest boxes at the four study sites available for the birds during the study period (see details in Supplementary Table S3.1). The number of nest boxes varied between years because a few nest boxes disappeared, or were removed, or relocated to new places (see Supplementary Table S3.1). We monitored a total of 100 to 233 great tit nests

annually, depending on nest box occupancy and we followed the field protocol, described in chapter 2.3. *General fieldwork*.

Shortly after fledging (typically within a few days, up to 2 weeks, after ringing) we carefully examined the nest material to identify and count the number of chicks that died in the nest after the time of ringing. We calculated the number of successfully fledged young ('number of fledglings' henceforth) as the number of nestlings ringed minus the number of ringed nestlings found dead in the nest after ringing.

We included only those breeding attempts in the analyses in which at least one chick hatched because the identity of the female was often unknown in broods that failed during the egg-laying or incubation stage (see above). There was no difference between habitats in the number of failed nests during this stage (urban sites: 52 nests, forest sites: 50 nests; chi-squared test of the habitat difference in the number of failed versus not failed clutches: $\chi^2 = 0.325$, $P = 0.569$, **DF = 1**). We regarded a brood as a first breeding attempt if it was initiated before the laying date of the earliest known second brood at that study site and year by a ringed female that fledged at least one young from her first brood in that year. The second brood period started when a ringed individual laid the first egg after a successful first brood at a particular site and year. If a female had only one clutch in a season, and this was started during the first brood period, we considered it as a single-brooded female in that year. We defined a female as double-brooded if it had a brood in the second brood period, and also had at least one nestling hatched in an earlier brood in the same year. Females sometimes used the same nest boxes for both their first and second broods, whereas they sometimes laid the second clutch in a different nest box. We detected double-brooding in both cases because we regularly checked unoccupied nest boxes through the whole breeding season. There was a temporal overlap between the termination of the last nesting attempt (we estimated that nestlings fledged out at age 19-21 days) in the first brood period (i.e. when the nestlings fledge from the nest) and the start of the first nesting attempt in the second brood period (i.e. when the first egg was laid) in all study sites (mean $\pm$ SD overlap, Veszprém: 12.86 ± 12.12 days, Balatonfüred: 8 ± 11.26 days, Szentgál: 11.71 ± 5.7 days, Vilma-puszta: 4 ± 5.9 days). Finally, we excluded broods that were the first known annual breeding attempts of identified females during the second brood period, because these females might have had a first brood that we did not detect (e.g. in natural cavities or nest boxes in private gardens) thus we cannot reliably decide whether these were single- or double-brooded females (number of excluded broods, Veszprém: 23, Balatonfüred: 9, Szentgál: 40, Vilma-puszta: 5). Our final sample size thus included 822 broods produced by 387 females (number of broods and females: Veszprém: 319/121; Balatonfüred: 134/70; Szentgál: 249/122; Vilma-puszta: 120/74).

Females could breed in more than one year, resulting in 585 female-year combinations (i.e. yearly breeding by the 387 females).

First, to analyse the difference in the probability of double-brooding between study sites, we used binomial generalized linear mixed-effects models with logit link function (package lme4 1.1-27.7 in R 3.4.4, Bates et al., 2015). The response variable was the females' annual breeding status (coded binary as 0: single- and 1: double-brooded), and the predictors were study site (four levels), female's age (FY or AFY), and the success of the first annual brood of the female (successful or failed after hatching). The fourth predictor was laying date (calculated as the number of days elapsed from 1 January until the laying of the first egg for each first brood, where day 1 = 1st of January) which was mean-centered separately for each site within each year (thus expressed the relative time of laying within a population in a particular year). We included the year and female ID as crossed random effects.

Second, to compare the probability of double-brooding between habitat types (urban versus forest) we used a pre-planned comparison (Ruxton & Beauchamp, 2008). To do this, we calculated an urban-forest linear contrast from the marginal means estimated for each study site in the above-described model (using the “contrast” function of the emmeans package, Lenth et al. 2019). Thus, we treated the four sites statistically as if they were two treatment groups and two control groups in an experiment, and we used a pre-planned comparison to test the prediction of whether the two treatment (i.e. urban) groups differ from the two control (i.e. forest) groups. With this method, we could test urban-forest habitat differences while controlling for the potentially confounding site effect without running into the statistical problems of having too few random factor levels, which would happen if the study site was included as a random factor in the model (Bolker et al., 2009; Piepho et al., 2003). Similarly, we used the same marginal means to conduct the following between-sites pairwise comparisons: Veszprém vs. Szentgál, Veszprém vs. Vilma-pusztá, Balatonfüred vs. Szentgál, and Balatonfüred vs. Vilma-pusztá (i.e., all urban vs. forest site pairwise comparisons). The P-values of these pairwise comparisons were adjusted using the false discovery rate (FDR) method.

Third, to analyse the number of fledglings produced annually by females (i.e., the number of chicks fledged from a female's first plus, if double-brooded, second broods) we used a generalized linear mixed-effects model with Poisson error distribution (package lme4). In this model, the response variable was the annual number of fledglings, and predictors were the female's annual breeding status (single- or double-brooded), study site (four levels), the breeding status $\times$ study site interaction, the success of the first seasonal brood of the female (successful or failed), and mean-centered laying date. We initially also included female age as

a further predictor, but we removed it from the model because it had no significant effect ($P = 0.818$), and removing it improved the model's fit (the model's AIC value decreased from 2861.9 to 2859.9). Female ID and year were included as crossed random factors. We used pre-planned comparisons of linear contrasts (as described above) to compare the annual number of chicks produced by females between urban and forest habitats. Besides, we conducted four more pre-planned pairwise comparisons between specific groups of females: (1) urban single-brooded females vs. forest single-brooded females and (2) urban double-brooded females vs. forest double-brooded females (to test the effect of habitat type within single- or double-brooded females, respectively), (3) urban double-brooded females vs. forest single-brooded females (to test whether double-brooded urban females can produce the same or higher number of nestlings than single-brooded forest females), and finally (4) we tested whether the differences in the number of fledglings between single- and double-brooded females differ between the two habitats.

Finally, to provide some background information on other components of reproductive success, we also analysed in two separate models (1) the total number of eggs and (2) the total number of hatchlings produced annually by females (i.e., the number of eggs and hatchlings produced in a female's first plus, if double-brooded, second broods). The model structure used in these analyses was similar to that described above for the analyses of the annual number of nestlings. We present these results as supplementary data (Appendix Table S3.2 and S3.3).

Results

Probability of double-brooding

During the study period, 44% of urban and 36% of forest females were double-brooded in at least one year. We found significant differences between the study sites in the probability of double-brooding (Figure 3.1, Table 3.1). The pre-planned comparison between urban and forest habitats (i.e., the two urban versus the two forest sites) indicated a marginally non-significant difference, with a trend for a higher probability of double-brooding in urban than forest birds (Table 3.2A). The pre-planned pairwise comparisons between urban and forest study sites revealed a significantly lower probability of double-brooding in Vilma-pusztá (forest) than in Veszprém (urban), whereas the difference between Vilma-pusztá and the other urban site, Balatonfüred was marginally non-significant. The other forest site, Szentgál, did not differ from either of the two urban sites in the probability of double-brooding (Table 3.2B, Figure 3.1).

We also found that AFY females had a higher probability of double-brooding than FY females (Figure 3.2 A). Double-brooded females laid their first eggs earlier than single-brooded females (Figure 3.2 B), and there was a marginally non-significant trend for a higher probability of double-brooding in females with failed seasonally first breeding attempts (Appendix Table S3.4).

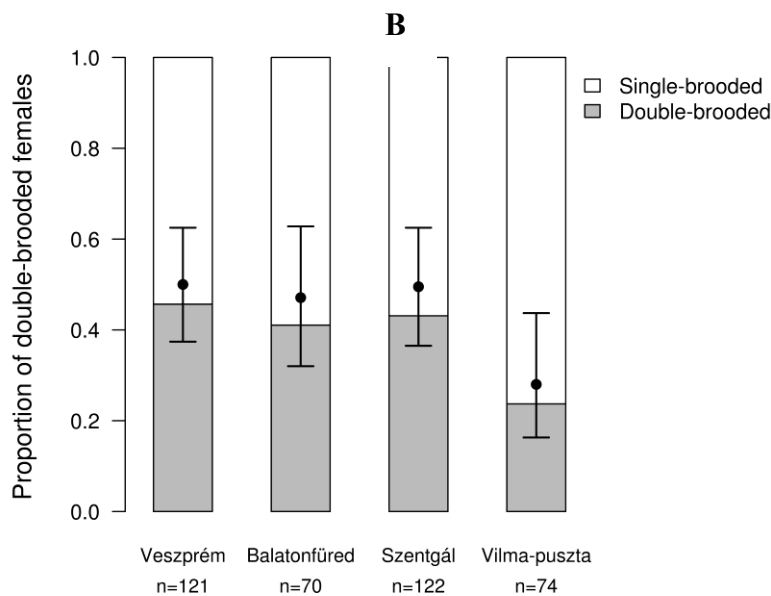


Figure 3.1. The proportion of double- versus single brooded female great tits at the four study sites (2013-2019; urban sites: Veszprém and Balatonfüred; forest sites: Szentgál and Vilma-pusztá). Black dots and associated whiskers show mean $\pm$ SE estimated by the binomial model (back-transformed from log odds ratio). Sample size (number of females) is presented below each box. Summary statistics for the model are presented in Appendix Table S3.4.

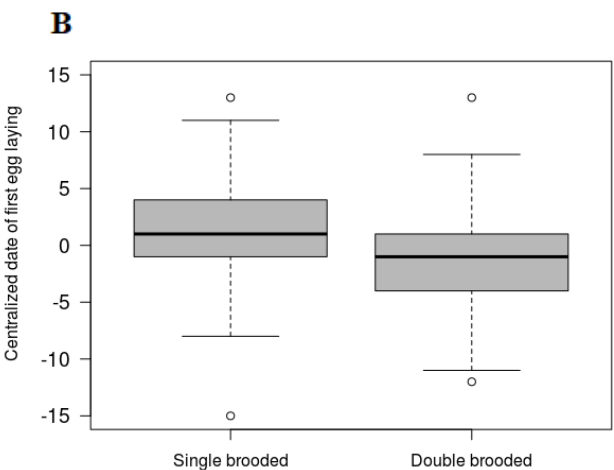
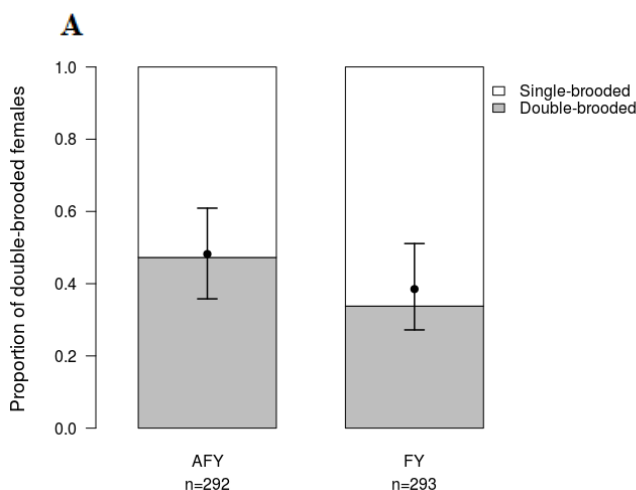


Figure 3.2. The effects of age and the laying date on the probability of double-brooding by female great tits. The table shows the results of the generalized linear mixed-effects model with binomial distribution (see Appendix Table S3.4 for parameter estimates).

Table 3.1. The effects of study site, female age, the success of the first seasonal brood, and laying date on the probability of double-brooding by female great tits. The table shows type 3 ANOVA results from the generalized linear mixed-effects model with binomial distribution (see Appendix Table S3.4 for parameter estimates). Statistically significant ($P < 0.05$) differences are highlighted in bold and marginally non-significant ($0.05 < P < 0.1$) differences are highlighted in italics.

	Chisq	df	P
Intercept	0.299	1	0.585
Study site	10.670	3	0.013
Female age	3.966	1	0.046
Success of first seasonal brood	3.372	1	<i>0.066</i>
Mean-centered laying date	30.428	1	< 0.001

Table 3.2. Differences in the probability of double-brooding between (A) habitat types and (B) study sites (urban sites: Veszprém and Balatonfüred; forest sites: Szentgál and Vilma-puszta). The table shows the results of linear contrasts that were calculated from the binomial model presented in Table 3.1. Contrasts are given as differences in log odds ratios. Odds ratio values are the exponentially back-transformed contrasts that provide the ratio of odds that a female being double-brooded in urban sites relative to forest sites (odds ratio > 1 indicate increased probability of double brooding in the urban habitat (A) or urban study sites (B), whereas odds ratio < 1 indicate increased probability of double-brooding in the forest). P-values were adjusted using the FDR method, statistically significant ($P < 0.05$) differences are highlighted in bold and marginally non-significant ($0.05 < P < 0.1$) differences are highlighted in italics.

	Comparisons	Contrast $\pm$ SE	Odds ratio $\pm$ SE	z ratio	Adjusted P
A)	Urban – Forest (habitat type)	0.426 $\pm$ 0.213	1.531 $\pm$ 0.327	1.995	<i>0.076</i>
B)	Veszprém – Szentgál (study sites)	0.021 $\pm$ 0.234	1.022 $\pm$ 0.239	0.092	0.927
	Veszprém – Vilma-puszta (study sites)	0.945 $\pm$ 0.305	2.572 $\pm$ 0.784	3.097	0.009
	Balatonfüred – Szentgál (study sites)	-0.093 $\pm$ 0.300	0.911 $\pm$ 0.273	-0.311	0.927
	Balatonfüred – Vilma-puszta (study sites)	0.830 $\pm$ 0.361	2.293 $\pm$ 0.827	2.302	<i>0.053</i>

Number of fledglings produced annually

We found that, as expected, double-brooded females produced more fledglings annually than single-brooded females (Table 3.3). The number of annually produced fledglings also differed between study sites, and there was a significant interaction between the effects of female breeding status (single- versus double-brooded) and study site (Table 3.3, Figure 3.3). The pre-planned comparison between habitats showed that urban females produced significantly fewer fledglings annually than their forest conspecifics (Table 3.4A), and this habitat difference was also present both within single- and double-brooded females (Table 3.4B, 3.4C). Furthermore, we found no significant difference in the number of fledglings between urban double-brooded and forest single-brooded females (Table 3.4D), indicating that urban double-brooded females produced about the same number of fledglings annually as forest females from a single brood (Figure 3.3). The difference in the number of fledglings between single- and double-brooded females was significantly greater in forests than in urban habitats (Table 3.4E).

Laying later in the season had a negative effect on the number of fledglings produced annually (Table 3.3, Appendix Table S3.5). Furthermore, females with failed first broods produced seasonally fewer fledglings than females with successful first breeding attempts (Table 3.3, Appendix Table S3.5).

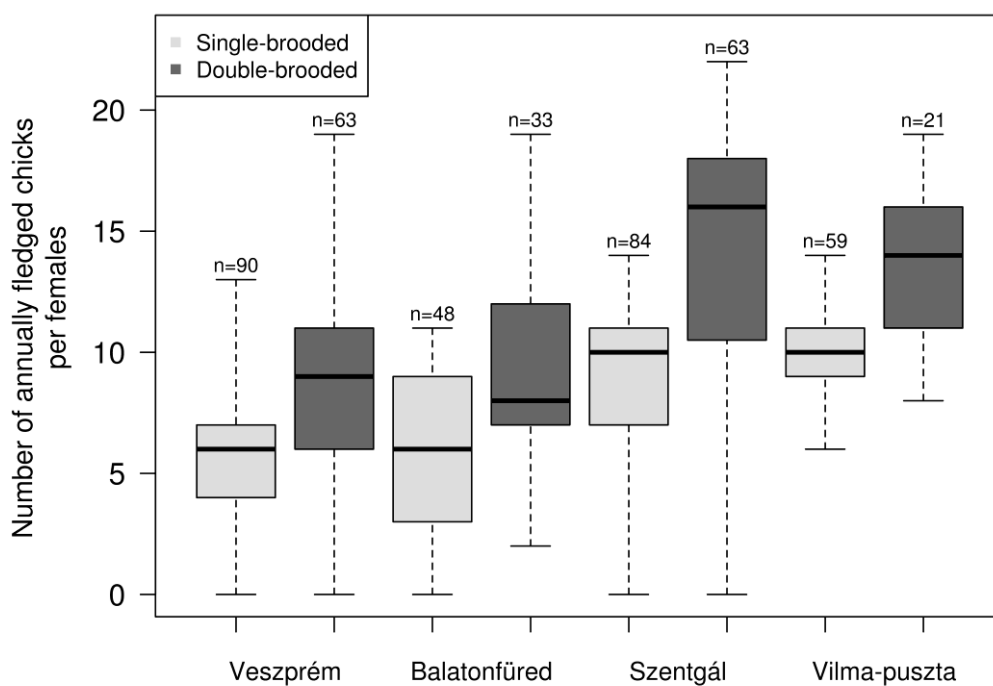


Figure 3.3. Differences in the number of fledglings produced annually by single- and double-brooded females in the four study sites (data pooled from all years). Urban sites: Veszprém and Balatonfüred; forest sites: Szentgál and Vilma-puszta. On the boxes medians and interquartile ranges are indicated by the thick middle lines and the boxes, respectively, while the whiskers extend to the most extreme data points within $1.5 \times$ interquartile range from the box. Sample size (number of females) is presented above each box. Females that were single-brooded in one year and double-brooded in another year, are included in both categories of the study site.

Table 3.3. The effects of female's annual breeding status (single- or double brooded), study site, the breeding status × study site interaction, the success of the first seasonal brood, and the laying date on the annual number of fledglings produced by females. The table shows the type 3 ANOVA results from the generalized linear mixed-effects model with Poisson distribution (see Appendix Table S3.5 for parameter estimates). Statistically significant ($P < 0.05$) differences are highlighted in bold.

	Chisq	Df	P
Intercept	17.846	1	<0.001
Female's annual breeding status	86.532	1	<0.001
Study site	149.287	3	<0.001
Success of first seasonal brood	147.554	1	<0.001
Mean-centered laying date	8.234	1	0.004
Female's annual breeding status × study site	10.692	3	0.013

Table 3.4. Differences between habitat types and female categories in the number of fledglings produced. The table shows the results of linear contrasts that were calculated from the model presented in Table 3.3. Contrasts are given as differences between the compared groups (on the natural logarithm scale). Ratio shows the exponentially back-transformed contrast estimates that provide the ratio of number of fledglings in urban sites compare to forest sites (ratio > 1 means that the number of fledglings is higher at the urban habitat, whereas ratio <1 means that the number of fledglings is higher at forest). Statistically significant ($P < 0.05$) differences are highlighted in bold.

Contrasts	Contrast ± SE	Ratio ± SE	z ratio	P
A) Urban – Forest, all females	-0.412 ± 0.031	0.663 ± 0.02	-13.242	<0.001
B) Urban – Forest, single-brooded females	-0.475 ± 0.042	0.622 ± 0.026	-11.221	<0.001
C) Urban – Forest, double-brooded females	-0.348 ± 0.045	0.706 ± 0.032	-7.683	<0.001
D) Urban double-brooded females – Forest single-brooded females	<0.0001 ± 0.041	1 ± 0.041	0.023	0.981
E) Urban single-brooded - double-brooded – Forest single-brooded - double-brooded	-0.126 ± 0.061	0.811 ± 0.054	-2.042	0.041

Discussion

Probability of Double-brooding

The lower reproductive success per breeding attempt in urban compared to rural bird populations is a well-documented phenomenon in many species (Chamberlain et al., 2009; Rodewald & Gehrt, 2014; Sepp et al., 2018). In urban landscapes, several environmental factors could increase the propensity of double-brooding (see Introduction), which in turn may significantly increase urban birds' overall reproductive output and hence may reduce the actual habitat difference in breeding success. Yet, the vast majority of studies published so far – including those on great tits – focused on seasonally first broods without considering multiple breeding attempts per season. Therefore, we used our long-term dataset to conduct a comprehensive comparison of the frequency of double-brooding between habitats and assessed its consequences on the annual reproductive success of females.

Contrary to our expectations, we found that the probability of double-brooding was not consistently higher in urban than in forest populations. Several features of the urban environments may explain these results. First, previous studies showed that high-quality food is often limited in cities during the breeding season (Marciniak et al., 2007; Nadolski et al., 2021), resulting in increased rates of starvation-related mortality and detrimental impacts on nestling development and fledging success (Seress et al., 2018, 2020). The relative scarcity of natural food sources may also limit urban birds' multi-brooding propensity (Batey, 2018; Verboven et al., 2001), either because females cannot find enough food to produce new clutches or because it is difficult and energetically expensive for the parents to provide enough prey items for their nestlings (Jarrett et al., 2020). The pre-fledging period could also be longer in urban habitats due to the slower development rate of nestlings (Corsini et al., 2020), which may eliminate the effect of seasonally earlier onset of breeding in cities. Additionally, if juvenile birds need increased or prolonged parental care during their post-fledging period, e.g. due to the difficulties of finding food sources independently, this could also decrease the probability of double-brooding for their parents (Grüebler & Naef-Daenzer, 2008; Verhulst & Hut, 1996). Finally, the propensity of double-brooding may also be at least partially a genetically determined trait, and the lack of sufficient genetic variation between populations may constrain changes in the tendency for double-brooding (Lindner et al., 2021; Timm et al., 2019; Watson et al., 2021).

Collectively, our results and the few other studies highlight that urbanisation has a highly variable effect on the frequency of double-brooding in urban bird populations. In great tits, Cowie and Hinsley (1987) found a higher number of second clutches in the city, whereas

Luniak et al. (1992) reported more second clutches in forests. In northern cardinals (*Cardinalis cardinalis*), there was no difference between urban and rural populations either in the number of the birds' annual nesting attempts or in their annual reproductive success (Leston & Rodewald, 2006). Acadian flycatchers (*Empidonax virescens*) in urban sites attempted fewer clutches and had a lower annual reproductive success than in rural habitats, perhaps due to the greater incidence of brood parasitism in the cities (Rodewald & Shustack, 2008). African crowned eagles (*Stephanoaetus coronatus*) breeding in more urbanised environments produced fewer fledglings per nesting attempt than birds breeding in less urbanised sites (similarly to the great tits in our study), but urban eagles had annually more nesting attempts which resulted in a similar annual reproductive success along the urbanisation gradient (Muller et al., 2020). The reasons for the heterogeneity between these results may include differences in local habitat conditions (Bartos Smith et al., 2016), and also ecological and life-history differences between species.

In our study, habitat heterogeneity might have contributed to the difference we found between the two forest sites in the probability of double-brooding. For example, these two sites have different tree species compositions (see Methods), which may influence the amount and seasonal distribution of phytophagous arthropods both during the egg-laying and the nestling development period. For example, caterpillar peak occurred one week later in Vilma-puszta than in Szentgál in two out of four years (see Table 3.1 in Seress et al., 2018). Furthermore, other cavity-nesting birds (e.g. blue tits *Cyanistes caeruleus*, collared flycatchers *Ficedula albicollis*, and Eurasian tree sparrows *Passer montanus*) frequently breed in the nest boxes in the forest sites, and the proportion of nest boxes occupied by these interspecific competitors may differ between the sites. Nest predation by european edible dormouse (*Glis glis*) and aesculapian snakes (*Zamenis longissimus*) is a common cause of brood loss in the forest populations and its frequency and seasonal dynamics could also differ between the sites. Interspecific competition and nest predation pressure can influence the frequency of double-brooding by affecting nest site availability, competition for food, and also the chance of rearing a second brood successfully. However, further studies are needed to understand the effects of these factors on the number of nesting attempts of great tits.

According to our results, those female great tits who start to breed earlier in the breeding season have a higher probability of double-brooding, which is in line with the findings of earlier studies conducted in other species (Bryant, 1979; Monroe et al., 2008, but see: Husby et al., 2009). Furthermore, older (i.e. AFY) females have a higher probability of double-brooding than FY females, which is likely related to the higher familiarity of the older birds with the available food sources, nesting sites, and to their improved skills to compete for these

resources (Hoffmann et al., 2015; Pigeault et al., 2020). The improved breeding performance with age may also be the consequence of the increase of reproductive effort with age, according to the residual reproductive value hypothesis (Williams, 1966; but see: Desprez et al., 2011). Moreover, failure of the first brood affected positively the initiation of a second clutch, which is a common phenomenon and probably works as a compensation strategy for the loss of the first clutch (Mulvihill et al., 2009; Tinbergen, 1987).

Number of Fledglings Produced Annually

Our results clearly showed that the annual number of fledglings was much lower in cities than in the forests, and the difference was present both within single- and double-brooded females. This result is in line with the findings of the earlier studies which compared the success of annual first broods between urban and forest breeding great tit populations (Bańbura & Bańbura, 2012; de Satgé et al., 2019; Markowski et al., 2015). In addition, our study showed that there was no significant difference in the average number of offspring between single brooded females in forest sites and double-brooded females in urban sites (suggesting that, urban females may need to produce two broods annually to have the same average number of offspring as the forest females could produce from a single brood).

We found that the later start of the first clutch within the breeding season has a negative effect on the number of annually fledged chicks, which is probably related to the decrease in food availability over the season (Batey, 2018; Seress et al., 2018). Unsurprisingly, females whose first clutch in the breeding season failed had seasonally fewer fledglings than females whose first clutch was successful. We also found a breeding status $\times$ study sites interaction (Table 3.3 and contrast E in Table 3.4), meaning that having a second brood had a different effect on the number of fledglings in different sites/habitats. Specifically, this result indicates that females in the cities can produce fewer additional offspring by a second brood than forest females (see Figure 3.2, and the negative contrast in Table 3.4). This result can be explained by the generally lower number of nestlings per brood in the urban sites, both in the first and the second broods.

The consistently lower annual number of nestlings in urban populations could lead to lower fitness (Carro et al., 2014; Tinbergen & Sanz, 2004) potentially resulting in a negative impact on population viability. Despite this, in some bird species including great tits population density is often similar or sometimes even higher in cities than in more natural habitats (Møller et al., 2012 and our unpublished data). This latter phenomenon implies that other mechanisms in cities may partly or completely compensate for the lower annual

reproductive success. For example, the milder climate (Grimmond, 2007) and the abundant human-provided food sources in cities could lead to better overwinter survival in urban compared to non-urban habitats (Evans et al., 2015; Robb et al., 2008; Sepp et al., 2018). Another possibility is that the high urban population densities are maintained by individuals dispersing from surrounding natural habitats into the cities. Unfortunately, the connectedness of urban and non-urban bird populations is poorly understood. The very limited evidence in tits, however, does not support a strong role of immigration in maintaining urban populations: for example, in a study conducted in Barcelona, migration appeared to be more prevalent from the city to the forest than vice versa (Björklund et al., 2010; Senar & Björklund, 2020). In sum, the low annual reproductive output of individuals in some urban bird populations makes the self-sustaining of these populations questionable and warrants further studies (Narango et al., 2018).

Our study has some limitations. First, we estimated the annual reproductive output of the females from the number of fledglings, but there are other proxies which can estimate fitness more accurately (e.g. the number of recruits). Second, the estimates of the frequency of double-brooding and the annual number of fledglings are based on data of females that bred in nest boxes. Since females occasionally breed in other nest sites (e.g. in cavities in trees and buildings) in both habitat types, some nesting attempts can remain undetected influencing the estimates of the reproductive output. Consequently, for a better understanding of the dynamics of urban populations, further long-term studies are needed on key demographic parameters, including multiple-brooding, first-year and adult survival, and migration between urban and non-urban habitats. Since the extent of urbanised areas is continuously increasing worldwide and urban areas hold significant populations of many bird species, such knowledge may help the future conservation of their populations.

4. Site-specific impacts of urbanization on annual survival of a forest bird

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This chapter is an extended and modified version of the research article “Boglárka Bukor, Brett K. Sandercock; Karl L. Evans, Ivett Pipoly; Krisztina Sándor; András Liker; Gábor Seress (2025) Site-specific impacts of urbanization on annual survival of a forest bird. Ecology and Evolution, 2025; 15:e71140. doi: <https://doi.org/10.1002/ece3.71140>”

Introduction

The conversion of natural and semi-natural habitats into human settlements is one of the key drivers of habitat loss and threats to global biodiversity (Beninde et al., 2015; Sol et al., 2017). Expansion of urban areas has complex and often negative effects on wildlife populations (Aronson et al., 2014; Ibáñez-Álamo et al., 2016), and the impacts will likely increase in the near future. Species richness and population density are commonly used metrics to characterize the overall impact of urbanisation on local wildlife communities (Aronson et al., 2017; Batáry et al., 2018), but quantifying demographic responses provides a more direct understanding of how urbanisation affects the viability of populations (Evans, 2010). A better understanding of demographic responses across the rural-urban gradient is therefore crucial if we are to preserve biodiversity in urban habitats (Banks, 2004; Crawford et al., 2018). It remains unclear, however, whether populations of species that have high densities in urban settings are self-sustaining or are maintained by immigration (Beninde et al., 2015; Chamberlain et al., 2009).

Ecological conditions and biological factors can vary across the rural-urban gradient, thus possibly lead to altered survival probabilities between urban and rural passerine populations. I discussed these processes in detail in chapter 1. *General introduction*.

Despite a large body of research that has explored how urbanisation influences particular selection pressures affecting mortality, our understanding of the cumulative impacts of the diverse drivers and thus how urbanisation shapes avian survival rates remains limited. The few studies that have been conducted reveal conflicting patterns, with some suggesting that urbanisation increases survival (Eden, 2021; Juárez et al., 2022; Phillips et al., 2018; Stracey & Robinson, 2012), while others have reported negative effects (Caizergues et al., 2022; Pharr

et al., 2023) or non-linear relationships with peak survival at intermediate levels of urbanisation (Evans et al., 2015). The variation partly stems from the differences in how individual species respond to urbanisation, with notable differences even between ecologically similar species (Evans et al., 2015; Marzluff, 2017). Furthermore, the environmental and ecological factors driving survival rates may significantly vary among years, but long-term studies of urban impacts on annual survival are rare (Murgui & Hedblom, 2017; Ouyang et al., 2018). Accurate assessments of how survival probability changes with urbanisation also require adequate spatial and temporal replication, as highlighted in recent theoretical reviews (Streby et al., 2014; Sepp et al., 2018; Ouyang et al., 2018).

In this long-term study, we use a temporally and spatially replicated mark-recapture dataset for great tits *Parus major*. Our objectives were to use mark-recapture data from two urban and two forest populations of great tits in Central Europe (Hungary) to test the impacts of urbanisation on avian survival rates and to examine whether the impacts of urbanisation are consistent among different urban environments.

Methods

Field methods

We monitored great tits breeding in nest boxes at two urban (Veszprém, Balatonfüred) and two forest (Szentgál, Vilma-pusztá) study sites, see the detailed description in chapter 2.2.

Study sites. During the 9-year study period of 2013-2021, we monitored a total of 100 to 235 great tit nesting attempts per year, depending on variation in breeding densities. Overall, between 293 and 353 nest boxes were available each year at the four study sites during the study period. During the fieldwork, we followed the protocol described in chapter 2.3.

General fieldwork.

During the chick-rearing period, the camera system enabled us to resight and reliably identify over 80% of breeding individuals each year without the need to recapture or handle birds (Seress et al. 2017). Additionally, we conducted occasional mist-netting to increase the number of colour-ringed birds in these populations. Thus, some of the birds were already ringed when we first observed them in our nestboxes and were subsequently added to this study (i.e., these mist-netted birds were included in the study only when they were observed as breeding parents). In our analyses, we excluded nonbreeding birds that were never observed during the breeding season. Breeding individuals regularly switch between nest

boxes within all of our four study sites; however, we never detected any dispersal movements of breeding individuals moving among the four study sites in the city or forest.

Statistical analysis

We estimated annual apparent survival (ϕ) and re-sighting probabilities (p) of adult great tits using Cormack–Jolly–Seber models in Program MARK version 10.0 (White & Burnham, 1999). We used data from colour-ringed adult birds to create encounter histories for each individual bird. We combined ringing data with re-sighting data from video recordings during the chick-rearing period and coded each year as detected (1) or not detected (0). Thus, the sampling period when data on detections of birds in the populations were collected corresponded to the 4-month breeding season of each year.

We analysed the live encounter data using two sets of CJS models. In the first set of models ('combined models'), we analysed the four study sites together. In the second set of analyses ('site-specific models'), we modelled apparent survival separately for each of the four study sites. Using this combined approach, our two goals were: (1) to determine if there were any site effects on apparent survival; and (2) to obtain a more detailed picture of how the different factors (age, sex, etc.) affected apparent survival at each site.

In the combined models, we modelled apparent survival from the four study sites in the 7 years between 2013 and 2019 when all sites were monitored simultaneously. We captured and marked a total of 907 adult tits during this study period; 340 (37.5%) of the birds were re-sighted or recaptured in at least one subsequent year. In the combined model set, we tested if apparent survival (ϕ) and re-sighting probability (p) were i) constant, ii) site-dependent in Veszprém (city), Balatonfüred (city), Szentgál (forest), or Vilma-puszta (forest), iii) time-dependent (with sequential time-periods defined as the period spanning from one breeding season to the next), iv) sex-dependent (male or female), or v) dependent on the site-specific breeding density (calculated separately for each year and site from the number of breeding pairs per the size of the study site (km²)) at a given time-period (providing a measure of population density). We also created several combinations of these five main effects with and without interactions, generating a total of 57 models (see the model list in the Appendix Table S4.1). In our analysis, the goal was to assess the effect of study site on apparent survival whilst taking into account variation among years, and sex and density dependence effects. We were unable to include the relative age of birds in the combined models because inclusion of age-dependence would result in model overfitting due to a high number of parameters resulting from the high number of factor-level combinations.

In the site-specific models for each of the four sites, we modelled apparent survival for the 9-year period between 2013 and 2021 at Veszprém, Szentgál, and Vilma-puszta; and between 2013 and 2019 at Balatonfüred, thereby maximising the number of observations available from the sites where the study continued after 2019. Our approach also allowed the inclusion of age-class in the analyses because a lower number of parameters had to be estimated for the site-specific than the combined models, thereby reducing problems arising from model overfitting. The number of birds, and the number of birds that were re-sighted in at least one subsequent year, were as follows: Veszprém (urban): $n=354$ (175, 49.4%); Balatonfüred (urban): $n=153$ (46, 30%); Szentgál (forest): $n=346$ (138, 49.9%); Vilma-puszta (forest): $n=186$ (69, 37.1%). In the site-specific models, we assumed that apparent survival (ϕ) might be i) constant, ii) age-dependent, iii) time period-dependent, or iv) sex-dependent (or any combination of these effects). In the age-dependent model, the apparent survival of FY individuals after first marking (ϕ_1) was treated separately from that of AFY individuals, but we did not make this distinction in subsequent years after FY birds had matured into the AFY age class (ϕ_2). If survival or site fidelity improve with age and experience, we expected that AFY birds would have higher apparent survival than FY birds. We considered re-sighting probability (p) to be i) constant, ii) time-dependent, or iii) sex-dependent (or any combination of these effects). In this set of analyses, we constructed $n = 57$ models in total for each site (see the model list in the Appendix Table S4.2-5). Parameter counts differed among sites because a shorter time series was available for Balatonfüred.

Unfortunately, but not surprisingly, several of the time-dependent models can not estimate the survival probabilities for some years ($SE=0$; see: Appendix Table S4.2-5). Therefore, we made a model selection for each site, without the time-dependent models. We present these results for each site too, in the Result chapter.

We tested for overdispersion in our data as a first step for each analysis. We fitted a global model that allowed apparent survival to vary as a function of site/age category, sex, and time-period (plus the breeding density in the combined model part) and the re-sighting probability to vary as a function of sex and time. We tested the fit of the global model for overdispersion in the data by estimating the variance-inflation factor ($\hat{c}$) using the Fletcher's c -hat procedure (Cooch & White, 2022) in Program MARK (Fletcher's $\hat{c} = 0.943$). We compared candidate models using the Akaike information criterion corrected for small sample sizes (AICc). We also conducted model averaging across all models per sites, to obtain overall weighted estimates for apparent survival (ϕ) and used model averaged values to illustrate our results.

Results

Combined models for all four study sites

These analyses included all four study sites, and three models were supported, i.e. two models had ΔAICc values < 2 relative to the one model with the lowest AICc value (Table S4.1). Effects of study site and year on apparent survival were supported by all three of these models (Table 4.1). The effect of sex was supported by one model with slightly higher apparent survival estimates for males than females, whereas none of these models supported an effect of breeding density on apparent survival (Table 4.1). The two urban study sites showed the greatest difference with the highest apparent survival in Veszprém but the lowest in Balatonfüred (Figure 3.1). The probability of apparent survival at the two forest sites was intermediate to the two urban sites in all years (Figure 3.1). We found evidence for large fluctuations in apparent survival among years. From 2017 to 2018, the best-fit models estimated an apparent survival probability of ~ 0.30 , which is half of the values estimated for the period with the highest apparent survival, 2016-2017. The probability of resighting was either constant (for model 1 and model 2: $p = 0.814 \pm 0.025$) or slightly higher in females (model 3: females, $p = 0.820 \pm 0.035$; males, $p = 0.808 \pm 0.033$; Table 4.1).

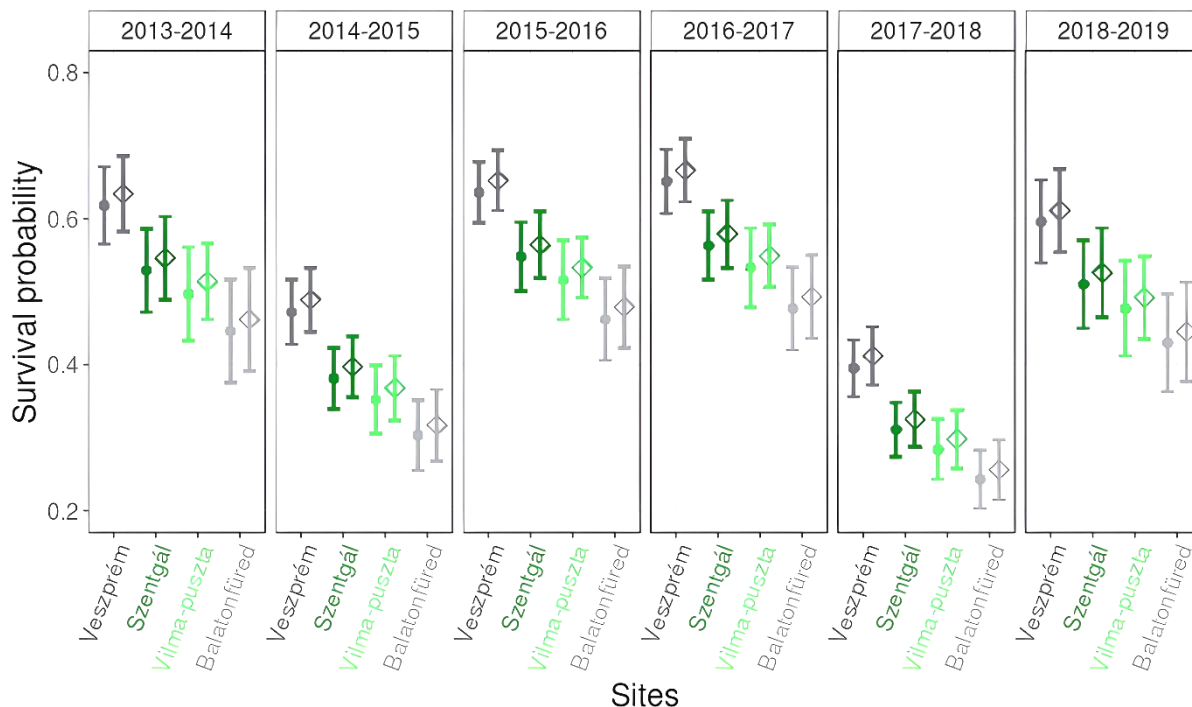


Figure 4.1. Model-averaged estimates from the combined models of annual apparent survival estimates (ϕ) for adult great tits in two urban (Veszprém, Balatonfüred; grey colours) and two forest sites (Szentgál, Vilma-puszta; green colours) between 2013–2019. Sites are ordered from highest to lowest survival estimates. The points and diamonds represent estimates of apparent annual survival (ϕ) and the whiskers represent standard error. The filled points show the survival probabilities for females, and the empty diamonds show the survival probabilities for males.

Table 4.1. Supported models from the combined set of models resulting from model selection of Cormack–Jolly–Seber capture-recapture analyses of data on breeding populations of adult great tits, at two urban sites (Veszprém, Balatonfüred) and two forest sites (Szentgál, Vilma-pusztá) between 2013 and 2019 (ϕ : apparent, annual survival probability; p : re-sighting probability). The supported models ($\Delta\text{AICc} < 2$) from the 57 Cormack–Jolly–Seber models containing the possible combinations of parameters are shown in order of AICc. Statistics given for each model include the Akaike information criterion corrected for small sample size (AICc), proportional support of the model (i.e. the AICc weight), number of parameters, likelihood (the AIC weight for the model of interest divided by the AIC weight of the best model in the browser) and deviance (deviance: $-2\log L(\theta)$ i.e. for a given model with parameters θ). The complete list of considered Cormack–Jolly–Seber capture-recapture models is shown in Appendix Table S4.1.

Model	AICc	ΔAICc	AICc weight	Model likelihood	Nr. of parameters	Deviance
1) $\phi(\text{site}+\text{time}), p(.)$	1874.516	0.000	0.331	1.000	10	294.045
2) $\phi(\text{site}+\text{sex}+\text{time}), p(.)$	1875.113	0.596	0.240	0.742	11	292.604
3) $\phi(\text{site}+\text{time}), p(\text{sex})$	1876.490	1.973	0.123	0.372	11	293.981

Site-specific models

Veszprém (urban)

Three models received similar support and had $\Delta\text{AICc} < 2$ (Table S4.2). All three models showed that apparent survival differed between the FY and AFY age categories. The survival of FY individuals (ϕ_1) varied among years and unexpectedly was usually higher than the apparent survival of AFY birds (ϕ_2) that was constant throughout the study period (Figure 4.2A, Figure 4.3, Table 4.2). One of the top models also showed sex dependence in apparent survival, indicating a slightly better apparent survival for males. The re-sighting probability was either constant (for model 1 and model 2: $p = 0.888 \pm 0.025$) or slightly sex-dependent (model 3: males, $p = 0.905 \pm 0.032$; females, $p = 0.869 \pm 0.039$). We fitted a global model and tested it for overdispersion with (Fletcher's $\hat{c} = 0.935$) and without time-dependence (Fletcher's $\hat{c} = 0.969$).

Without the time-dependent models, two out of the 12 models had $\Delta\text{AICc} < 2$ (Table S4.6). Similarly to the time-dependent models, both showed a difference between age categories, and sexes. The re-sighting probabilities were sex-dependent in one model (Figure 4.7) and constant in the other one.

Balatonfüred (urban)

Two competing models had $\Delta\text{AICc} < 2$ (Table S4.3). Apparent survival differed between the FY and AFY age categories in both models, with FY birds again tending to have higher

survival than AFY birds in most years (Figure 4.2B). Model 1 indicated constant apparent survival for ϕ_1 with time and sex effects on ϕ_2 (slightly higher apparent survival estimates for males than females; Figure 4.2B, Figure 4.4, Table 4.2). However, model 2 showed sex-dependent apparent survival for ϕ_1 and constant apparent survival for ϕ_2 (Table 4.2). The re-sighting probability was constant in the first model ($p=0.837\pm0.084$), but time-dependent in the second model (Table 4.2). We fitted a global model and tested it for overdispersion with (Fletcher's $\hat{c} = 0.898$) and without time-dependence (Fletcher's $\hat{c} = 1.037$).

Without the time-dependent models, four models had $\Delta AIC_c < 2$ (Table S4.7). Analogous to the time-dependent models, all the four models showed that apparent survival differed between the FY and AFY age categories. The re-sighting probabilities were sex-dependent in one model (Figure 4.7) and constant in the other three supported models.

Szentgál (forest)

Three competing models had similar support with $\Delta AIC_c < 2$ (Table S4.4). Unlike the two urban sites, the best-fit models did not include an age effect on apparent survival (Table 4.2). Two out of three models indicated effects of sex (slightly higher apparent survival estimates for males than females) and inter-annual variation in apparent survival, and one model included only inter-annual variation (Figure 4.2C, Figure 4.5). Re-sighting probability was time-dependent in one model and time and slightly sex-dependent in the other two models (Table 4.2). We fitted a global model and tested it for overdispersion with (Fletcher's $\hat{c} = 0.958$) and without time-dependence (Fletcher's $\hat{c} = 1.035$).

Without the time-dependent models, five (out of 12) had similar support with $\Delta AIC_c < 2$ (Table S4.8). Four of the five supported models showed no age differences in the survival, similarly to the time-dependent models. One supported model showed age differences and no sex differences of the survival, neither the re-capture probability. The re-sighting probabilities were sex-dependent in two model (Figure 4.7) and constant in the other three supported models.

Vilma-puszta (forest)

Three competing models had $\Delta AIC_c < 2$ (Table S4.5). Similar to the other forest site, the top models did not include any age effect on apparent survival (Table 4.2). Two out of the three supported models show constant apparent survival during the study period, whereas the third one indicated a sex effect with slightly higher apparent survival probability for males than females (Figure 4.2D; Figure 4.6, Table 4.2). The re-sighting probability was time-dependent

in all three models, with two of these also having a sex effect (Table 4.2). We fitted a global model and tested it for overdispersion with (Fletcher's $\hat{c} = 0.973$) and without time-dependence (Fletcher's $\hat{c} = 1.022$).

Without the time-dependent models, four models had $\Delta AIC_c < 2$ (Table S4.9). The pattern here is similar to the Szentgál site. Three of the four supported models showed no age differences in the survival, similarly to the time-dependent models. One supported model showed age differences and no sex differences in survival. The re-sighting probabilities were sex-dependent in one models (Figure 4.7) and constant in the other three supported models.

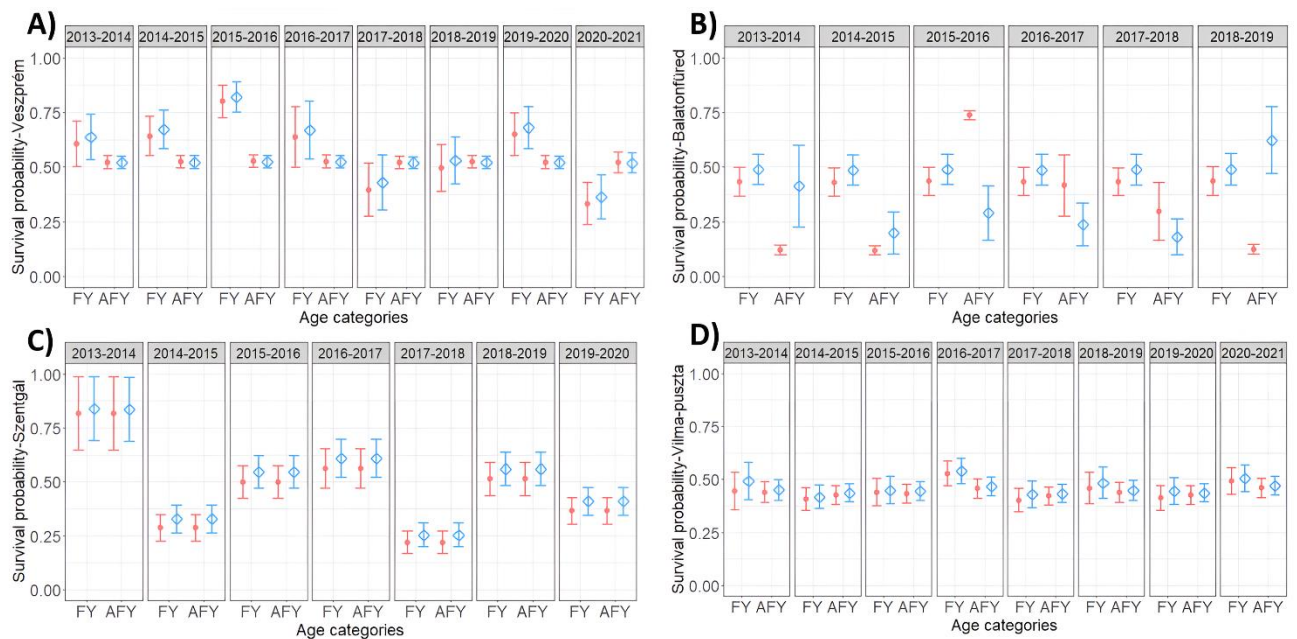


Figure 4.2. Model-averaged estimates from the site-specific models of annual apparent survival estimates (ϕ) for adult great tits in A) Veszprém (city), B) Balatonfüred (city), C) Szentgál (forest) and D) Vilma-pusztá (forest). The last transition from Szentgál is removed from the figure (because both the ϕ and p have time dependence, and the last transition is nonidentifiable here). The symbols indicate the estimates of ϕ : the red filled points represent female survival and the blue hollow squares represent male survival; whiskers represent standard error. FY: first-year breeder = hatched in the previous calendar year (ϕ_1); AFY: having at least one breeding season before the current one = hatched at least two years prior (ϕ_2). hatched at least two years prior (ϕ_2).

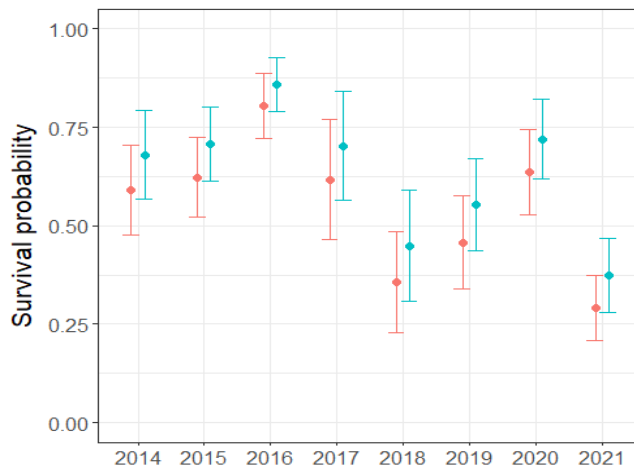


Figure 4.3. Survival probability estimates of FY birds in Veszprém. This figure show the results of the following supported model: $\phi 1\text{-FY}(\text{sex}+\text{t})$. $\phi 2\text{-AFY}(\text{con})$. $p(\text{con})$; $\Delta\text{AIC}=0.738$

The symbols indicate the estimates of ϕ : the red filled points represent female survival and the blue hollow squares represent male survival; whiskers represent standard error.

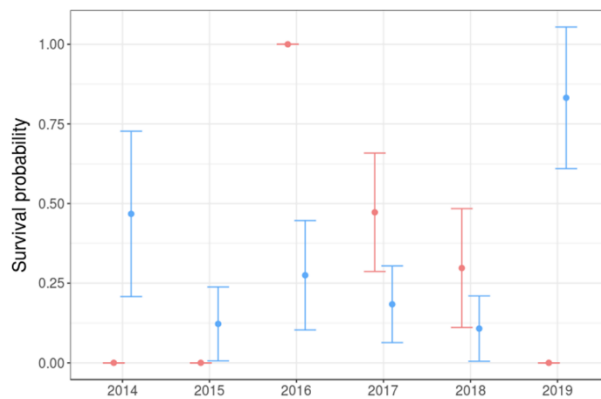


Figure 4.4. Survival probability estimates of AFY birds in Balatonfüred. This figure show the results of the following supported model: $\phi 1\text{-FY}(\text{con})$. $\phi 2\text{-AFY}(\text{sex}*\text{t})$. $p(\text{con})$; $\Delta\text{AIC}=0.000$

The symbols indicate the estimates of ϕ : the red filled points represent female survival and the blue hollow squares represent male survival; whiskers represent standard error.

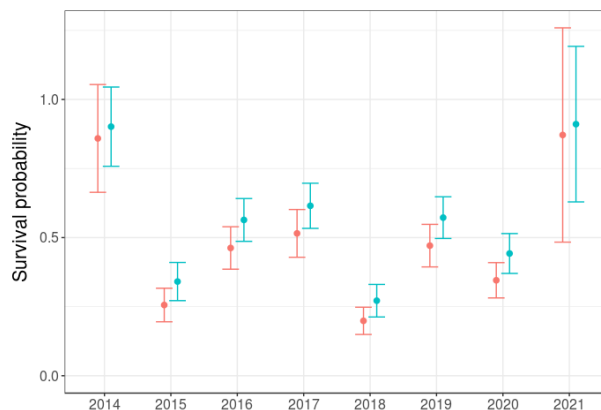


Figure 4.5. Survival probability estimates from Szentgál. This figure show the results of the following supported model: $\phi (\text{t}+\text{sex})$ $p(\text{t}+\text{sex})$; $\Delta\text{AIC}=0.654$

The symbols indicate the estimates of ϕ : the red filled points represent female survival and the blue hollow squares represent male survival; whiskers represent standard error.

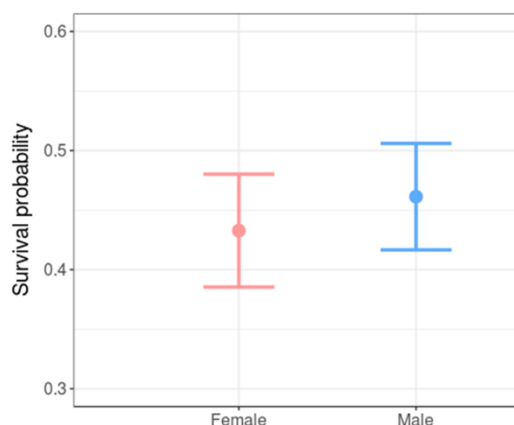


Figure 4.6. Survival probability estimates from Vilma-pusztá. This figure show the results of the following supported model: $\phi (\text{sex})$ $p(\text{t}+\text{sex})$; $\Delta\text{AIC}=1.941$

The symbols indicate the estimates of ϕ : the red filled points represent female survival and the blue hollow squares represent male survival; whiskers represent standard error.

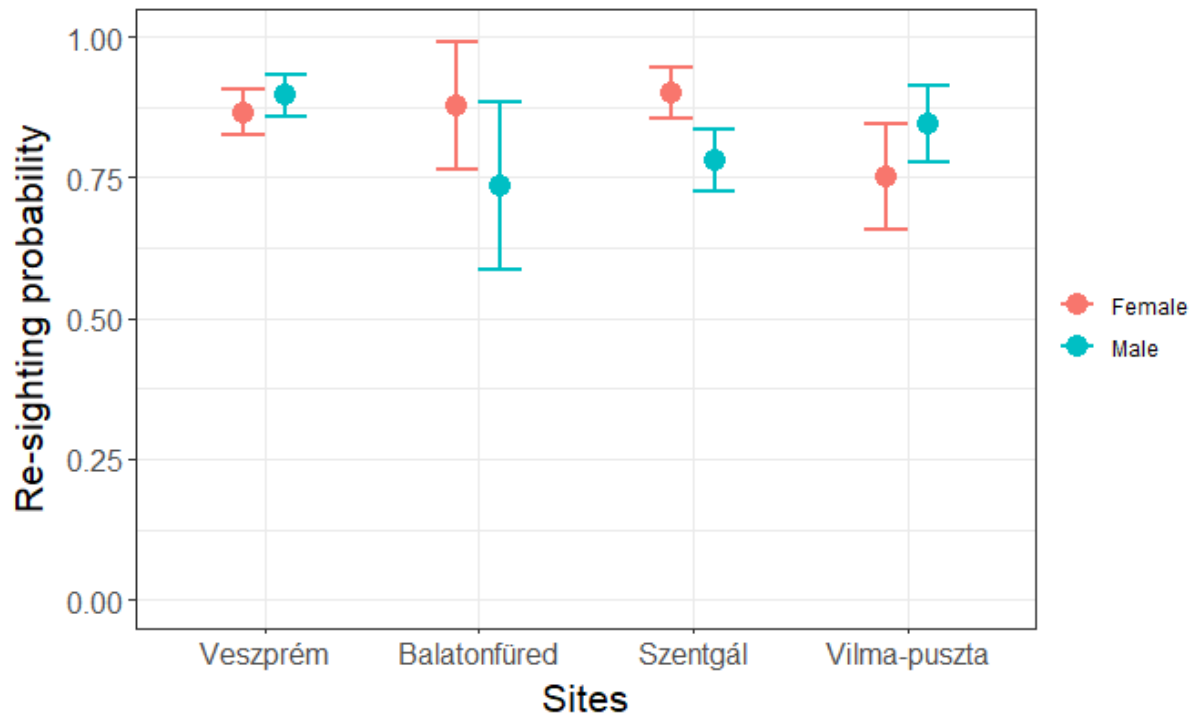


Figure 4.7. Sex-dependent re-sighting estimates of the probability for the four study sites. The estimates presented here are derived from site-specific model sets, without incorporating time-dependent models. The estimates for each site are from the following models:
 Veszprém: ϕ 1(sex), ϕ 2(sex), p (sex); $\Delta AICc$ = 1.739; Balatonfüred: ϕ 1(sex), ϕ 2(constant), p (sex); $\Delta AICc$ = 1.55; Szentgál: ϕ (sex). p (sex); $\Delta AICc$ = 0.489; Vilma-pusztá: ϕ (constant). p (sex); $\Delta AICc$ = 1.372.

Table 4.2. Supported models resulting from model selection of Cormack–Jolly–Seber capture-recapture analyses for data on breeding populations of adult great tits at our four study sites separately: Veszprém (city), Balatonfüred (city), Szentgál (forest) and Vilma-pusztá (forest). ϕ : apparent, annual survival probability; p : re-sighting probability. The supported models ($\Delta AICc < 2$) from the 57 Cormack–Jolly–Seber models containing the possible combinations of parameters are shown in order of AICc. Statistics given for each model include the Akaike information criterion corrected for small sample size (AICc), proportional support of the model (i.e. the AICc weight), number of parameters, likelihood and deviance (deviance: $-2\log L(\theta)$) i.e. for a given model with parameters θ). The complete list of considered Cormack–Jolly–Seber capture-recapture models is shown in Table S2-S5. The apparent annual survival of FY individuals in their first year (ϕ_1) was considered to differ from that of AFY individuals, but we did not make this distinction in subsequent years, i.e. when FY birds moved to the AFY age class (ϕ_2).

Study-site	Model	AICc	$\Delta AICc$	AICc weight	Model likelihood	No. of parameters	Deviance
Veszprém [←] (urban)	1) $\phi_1(\text{time}), \phi_2(.); p(.)$	935.029	0.000	0.278	1.000	10	173.368
	2) $\phi_1(\text{sex+time}), \phi_2(.); p(.)$	935.768	0.738	0.192	0.691	11	172.029
	3) $\phi_1(\text{time}), \phi_2(.); p(\text{sex})$	936.596	1.566	0.127	0.456	11	172.858
Balatonfüred [←] (urban)	1) $\phi_1(.), \phi_2(\text{sex*time}); p(.)$	242.270	0.000	0.467	1.000	10	51.477
	2) $\phi_1(\text{sex}), \phi_2(.); p(\text{time})$	244.047	1.776	0.192	0.441	6	62.095
Szentgál [←] (forest)	1) $\phi(\text{sex+time}); p(\text{time})$	754.027	0.000	0.265	1.000	15	144.034
	2) $\phi(\text{time}); p(\text{time})$	754.351	0.323	0.225	0.850	14	146.486
	3) $\phi(\text{sex+time}); p(\text{sex+time})$	754.682	0.654	0.191	0.720	17	140.405
Vilma-pusztá [←] (forest)	1) $\phi(.); p(\text{sex+time})$	391.352	0.000	0.250	1.000	7	126.029
	2) $\phi(.); p(\text{time})$	391.780	0.428	0.201	0.803	6	128.571
	3) $\phi(\text{sex}); p(\text{sex+time})$	393.293	1.941	0.094	0.378	8	125.839

Discussion

We used live encounter data of breeding birds attending nests to estimate apparent annual survival of adult great tits at two urban and two rural sites across multiple years. Our long-term field study and analyses yielded three major findings. First, we did not find consistent differences in the apparent survival estimates of great tits between urban and forest sites. Instead, both the set of combined models with all four study sites together and the site-specific models confirmed that urban sites had both the highest (Veszprém) and the lowest (Balatonfüred) estimates of apparent survival (but, in the case of location-specific models, the picture is somewhat more nuanced). Specifically, in Veszprém the average annual survival was roughly ~ 0.57 while in Balatonfüred it was ~ 0.4 . The two forest sites had intermediate annual apparent survival compared to the two cities (with ~ 0.47 in Szentgál and ~ 0.45 in Vilma-pusztá). Our finding illustrates the heterogeneity of urban areas, contrasting with prevailing viewpoint that towns and cities are homogeneous environments (Bartos Smith et al., 2016). Moreover, it clearly demonstrates a need for urban ecology research to assess patterns at multiple sites (Kinnunen et al., 2022). Second, our results also highlighted considerable inter-annual variation in apparent survival probabilities on our study populations. Variation in demographic rates underscores the importance of assessing urbanisation impacts over multiple years. Last, our site-specific analyses also revealed that the survival rates possibly could be reduced among older birds (FY versus AFY) in urban environments, but not necessarily in forests. Survival rates typically improve with after the first breeding season, compared to the time-period before the first breeding season. Declines are compatible with theoretical models of how urbanisation influences actuarial senescence (Watson et al., 2015) but empirical tests on long-lived raptors have failed to support this hypothesis (Sumasgutner et al., 2019). In combination, these findings suggest that the processes determining apparent survival probabilities vary across urban and more natural habitats in a complex manner.

Limitations of the study

We used Cormack-Jolly-Seber models based on live encounter data to estimate the annual probability of apparent survival, and like all studies using mark-recapture methods in open populations, it is extremely difficult to distinguish mortality from permanent emigration from the study areas. To mitigate the potential biases stemming from this, we excluded hatch-year birds from our dataset because natal dispersal of juveniles away from their site of birth to their first breeding site is quite common in songbirds (Könczey et al., 1997). On the contrary, breeding adults typically exhibit strong site fidelity and reoccupy their territory from the

previous year (Harvey et al., 1979). Great tit breeding dispersal typically only occurs over small distances (Harvey et al., 1979), and we consider that such events are unlikely to bias our conclusions regarding between-site variation in survival rates for several reasons. First, our previous results showed no significant difference in the nest box fidelity of breeding females between years across the four study sites (Bukor, 2017). Second, due to the structure of public green spaces, the urban study site at Veszprém comprises multiple nest-box sites, contrasting with the single and more evenly shaped urban park, with one site for the nest-boxes in Balatonfüred (Figure S4.1). Therefore, all other things being equal, a dispersing bird is more likely to permanently emigrate from the Veszprém (to nearby private gardens) than the Balatonfüred study site. Yet we found higher apparent survival rates at Veszprém, suggesting that the differing estimates of apparent annual survival for the two cities are not unduly influenced by emigration from our study area. Last, both survival (to a certain point) and site fidelity of the passerines are expected to increase or stagnate with age but apparent survival of urban birds actually decreased among older tits at urban but not forest sites (Bouwhuis et al., 2012; Fay et al., 2020; Gyurácz et al., 2021; Orell & Belda, 2002).

Our combined models indicated that the birds' re-sighting probability was constant in two out of three supported models, while slightly higher for females in the third one ($p > 0.8$ in all of these models). A marginal difference in detectability between sexes is probably explained by our data collection protocol. Specifically, during nest checks, the likelihood of finding one of the parent birds on the nest – and thus identifying it by its colour rings – is likely to be higher for females because they are the sex that is more likely to remain on the nest during incubation or brooding period (Vincze et al., 2021). Additionally, when capturing birds on their nest, we targeted female over male parents in situations where we had to choose which individual to capture because we focused on females for some of our other study objectives. Nevertheless, the overall high re-sighting probabilities are consistent with our intensive nest monitoring programme and the use of the camera system for identifying individual birds, confirming that we could successfully identify the majority of adults breeding in the nest boxes.

Differences among sites and habitats

Our results provided no evidence that survival rates of songbirds were consistently higher in urban environments, which was in contrast with previous studies (Juárez et al., 2022). Several factors may explain higher spatial heterogeneity among urban sites. First, the availability of insect larvae and other important natural food sources is markedly lower in cities compared to

forests, with less pronounced peak abundances throughout the season (Marciniak et al., 2007; Nadolski et al., 2021; Seress et al., 2018). Adult birds may compensate for lower availability and less predictable natural food sources in urban areas by exploiting anthropogenic food sources (Sinkovics et al., 2021, 2023). However, the availability of alternative food sources, such as bird feeders, trash bins, and pet or domestic animal food, depends on local conditions and is likely to vary widely between urban areas (Tryjanowski, Skórka, et al., 2015). For instance, in the winter of 2021–2022, the mean density of active bird feeders in the Veszprém study site was 126.3 feeders / km² (Bukor et al, in prep.), and while we do not have comparable data for Balatonfüred, supplemental feeding is likely to be lower since most of the site was parkland with a lower density of people (especially during winter, Balatonfüred being a summer holiday area) and fewer inhabited houses in the study site. Therefore, while some urban locations may offer abundant anthropogenic food sources, potentially increasing the annual survival of birds above conditions in natural habitats (Sepp et al., 2018), supplementary resources may be scarcer in other urban areas. In the latter case, birds may either maintain lower body reserves with less fat, increasing the risk of starvation under adverse weather conditions, or may be forced to move more searching for food, increasing the risk of predation-related mortality (Baker et al., 2005; Loss et al., 2015; van Heezik et al., 2010).

Second, cities may also differ in predator densities which could have a strong impact on adult survival rates. Several raptors known for hunting small birds, such as the Eurasian sparrowhawk (*Accipiter nisus*), the Eurasian goshawk (*A. gentilis*), and the common kestrel (*Falco tinnunculus*) have successfully colonised European cities (Merling De Chapa et al., 2020; Millsap, 2018; Thornton et al., 2017). Additionally, domestic predators like feral cats are extremely abundant in some urban areas (Loss et al., 2015; Loss & Marra, 2017) posing a significant threat to adult birds (Baker et al., 2005; Bonnington et al., 2013). Since the characteristics of local predator communities could differ between our study sites, predation pressure may also be involved in generating the heterogeneity of apparent survival rates we found between the two cities involved in our study.

Last, microclimatic conditions can also influence the survival rate differences among urban bird populations. For example, the urban heat island effect, which is more pronounced in larger cities (Climate Central, 2021), acts as a buffer against the effects of cold weather conditions, potentially enhancing winter survival in more urbanised areas. Previous research has found that milder winters contribute to higher adult survival rates in several passerine species (Dybala et al., 2013; Salewski et al., 2013). However, this explanation is probably not applicable to our study sites, as Balatonfüred (the site with the lowest apparent survival

estimates) was actually the warmest site among our study locations. On the other hand, urban heat island effects can intensify the effects of extreme temperature events, such as summer heat waves, thereby increasing heat stress in more urbanised areas (Xie et al., 2017). Previous studies have shown that escalation of summer heat waves can increase adult mortality rates in both desert and temperate species (Gardner et al., 2017; McKechnie et al., 2021; Lv et al., 2023), but the degree of impact varies significantly among species (Robinson et al., 2007; Gullett et al., 2014). According to this finding, the increased mortality due to heat stress in Balatonfüred, relative to the other study sites, could partially account for the consistently lowest survival rates we found at this site (Figure 4.1).

Differences between age groups

Our site-specific models revealed that age significantly influenced apparent survival at both urban sites, but the pattern was absent in the forest sites. Unexpectedly, in several years, FY (younger) birds had higher apparent survival than AFY (older) birds in urban habitats. The difference is align with previous findings indicating urban environments impose significant stress on reproductive effort, leading to high mortality rates of nestlings due to starvation (Seress et al., 2018, 2020) and strong selection during the early development stage (Corsini et al., 2020). Such environmental stress is further evident in the shorter telomere of urban nestlings, suggesting a reduced lifespan (Salmón et al., 2016), with similar early-life stress effects reported in other wild bird species exposed to urban-like stressors (Meillère et al., 2015). Early-life adverse conditions likely compromise the long-term survival prospects of urban birds (Salmón et al., 2017). Urban FY individuals in our study, having survived their first breeding season, represent birds who were the ‘winners’ of the strong selection during their early life stages, contrasting to AFY birds (already in their 3rd calendar year or older) that might have already faced age-related physiological declines and therefore decreased chance of survival. This result supports what Saulnier et al (2023) suggest, that “*cities act as a filter in which only good quality individuals survive and achieve successful reproduction regardless of year*”. In forests, where early-life selection is less pronounced, survival rates across age groups might be relatively similar, as we have found in our forest great tit populations.

Another explanation for the observed higher apparent survival in the FY group could be that these birds have had lower reproductive investment and bred only in a single year compared to AFY birds that bred in multiple years, and the difference could be more pronounced in urban environments. Previous research indicates that increased parental investment can detrimentally affect subsequent survival. For example, the survival rate of

female great tits was found to increase when their seasonally second clutches were experimentally removed (Verhulst, 1998). This hypothesis may be particularly relevant for great tits, as studies have found that the survival rate of female willow tits (*Poecile montanus*) significantly decline after reaching five years of age, while such an effect was not present in males. Recent studies also revealed that great tits experienced a reduction in telomere length between winter and the subsequent reproduction in the urban but not in the forest habitat (Saulnier et al., 2022), despite urban birds' generally better tolerance for stressful conditions (Costantini et al., 2014; Walther & Barber, 2020). These findings suggest that the demographic costs associated with breeding may emerge in later life stages, highlighting the intricate trade-off between reproductive investment and survival in birds that might also be affected by breeding habitat type.

Similarly to our results, a study on four blue tit populations from the same Mediterranean region found a consistently higher survival for first-year versus older birds in forested areas (Bastianelli et al., 2021). But, another recent study in France found contrasting results as they found no significant difference between first-year and adult great tits' survival probabilities at an urban site and reported the highest survival for forest yearling birds (Caizergues et al., 2022). The comparison of these two studies to ours is not straightforward, however, due to the different age-categorization applied, and because in previous studies yearling birds' survival estimates might have been confounded by yearling birds' natal dispersal.

Differences between the sexes

The effect of sex appeared in some of the models for each study site, and also in our combined models, indicating slightly higher survival for males than females both in our forest and urban sites. Our findings are consistent with several previous studies on great tits (Clobert et al., 1988; Forero et al., 2001; Masoero et al., 2016; Callery et al., 2022;), although some mark-recapture studies reported no significant difference between sexes (Caizergues et al., 2022), or even slightly higher apparent survival in females (Horak & Lebreton, 1998).

In birds, the adult sex ratio tends to be biased towards the homogametic sex (males) due to the higher mortality rate of the heterogametic sex (females; Pipoly et al., 2015; Székely et al., 2014). Sex differences are often explained by the higher reproductive costs faced by females, including egg-laying and more intensive brood care, which could reduce their survival probability (Romano et al., 2022; Verhulst, 1998). Despite this general pattern, our results, suggesting higher reproductive costs for females relative to males in both habitat types. Females may also be more vulnerable to being trapped by predators in the nest cavity. Here,

nest predation was more common at our forest study sites, especially during second broods (mainly due to the edible dormouse *Glis glis*; our unpublished data), and such events often also result in the death of the female parent. Therefore, while the mechanisms leading to the slight sex-specific differences in apparent survival may differ between our urban and forest study sites, our findings suggest that the combined effects of these factors ultimately balance out between habitats. The balance results in the slightly higher survival prospects for males, a difference that has been observed in many previous studies.

Annual variation in apparent survival

Apparent survival of adults showed high variation among years according to our models. In the site-specific model sets, a high year-to-year variation in apparent survival was present in the supported models in Veszprém (urban), Balatonfüred (urban), and Szentgál (forest), but not in Vilma-pusztá (forest). However, the relatively low annual sample sizes we were able to use for Vilma-pusztá, can hinder the detection of a presumably low (lower than the other three sites) annual variance.

Adult survival also could vary among years due to long-term population trends (Siriwardena et al., 1998). Large year-to-year fluctuation of survival is a common phenomenon in small-bodied species that may be more sensitive to environmental effects (Healy et al., 2014). Annual changes in the survival of adult birds are highly influenced by complex environmental factors, like disease (Jiménez-Peñuela et al., 2019; Lawson et al., 2012), prevailing weather conditions (Dybala et al., 2013; Lv et al., 2023) and fluctuations in natural food supply (Callery et al., 2022; Grøtan et al., 2009). Unfortunately, we do not have additional data for these environmental variables throughout the study period to evaluate whether they were involved in generating the annual fluctuations we detected.

Conclusions

In this study, we found contrasting patterns of apparent survival among urban bird populations: lower survival in one urban location compared to forested areas, and higher in the other urban site. Our results indicate substantial variability in avian survival rates across different urban environments, even among nearby sites. Therefore, our study highlights a common limitation in research design that compares only a single pair of urban and rural study sites. Had our analysis been restricted to a single urban location, we could have inaccurately inferred that urbanisation either enhances or diminishes the survival prospects of great tits relative to forested habitats. Our study thus emphasizes the critical need for future

research to include multiple urban and rural settings (Ouyang et al., 2018), as various local socioeconomic factors could influence the factors governing urban birds' annual survival rates (Kinnunen et al., 2022). Last, the observed habitat-related age effect on survival underscores the possible impact of urbanisation on passerine senescence processes – an important implication that requires further research to be explored. In conclusion, our result suggests that different factors influence the apparent survival of adult birds in urban than in natural habitats, and it will be the task of upcoming studies to identify these specific factors and their effects on survival probabilities.

5. Radio-tracking urban breeding birds: the importance of native vegetation

Gábor Seress; Krisztina Sándor; Veronika Bókony; Boglárka Bukor; Katalin Hubai; András Liker

This chapter is an extended and modified version of the research article “Gábor Seress, Krisztina Sándor; Veronika Bókony; Boglárka Bukor; Katalin Hubai; András Liker (2025) Radio-tracking urban breeding birds: the importance of native vegetation. Ecological Application, 2025;35:e3095. doi: <https://doi.org/10.1002/eap.3095>”

Introduction

Several features of the urban ecosystems can contribute to the lack of insects in our cities and towns, the drastic alteration and management of vegetation probably play a key role (Jensen et al., 2022; Jones & Leather, 2012; Narango et al., 2018). The altered urban flora contributes to the reduced arthropod abundance in at least two main ways. First, the diminished and fragmented vegetation cover in urban areas creates physical patchiness, limiting foraging sites for phytophagous arthropods and suitable locations for their larvae to develop, pupate, or overwinter (Jones & Leather, 2012). In such habitats, birds should spend more time and energy on traveling greater distances to feed their offspring. Indeed, this pattern was documented for great tits and blue tits (*Cyanistes caeruleus*) by Hinsley et al. (2008) who found that parents in patchy urban habitats had 64% higher energy expenditure per chick raised compared to continuous woodlands. Similarly, tracking blue tit parents by radio-telemetry, Jarrett et al. (2020) reported that birds in urban parks travelled farther when foraging for nestling food than those breeding in a forest. This increased parental workload probably results in fitness costs for parent birds such as lower survival rates or reduced clutch size, although such impacts were not quantified in these studies.

Second, urban green spaces, despite their vegetation cover, often lack suitable foraging habitats due to their high heterogeneity and functional patchiness (Mackenzie, 2010). The majority of herbivorous insects have strong coevolved relationships with one or a few closely related plant lineages, resulting in tight links between the abundance of phytophagous arthropods and that of their preferred host plants (Brändle & Brandl, 2001; Forister et al., 2015; Tallamy & Shriver, 2021). In urban environments, people often favour non-native over

native plants (Aronson et al., 2014) for their aesthetic appeal, ease of maintenance, commercial availability, or stress tolerance. However, non-native vegetation supports significantly less diverse and less abundant arthropod communities (Jensen et al., 2022; Narango et al., 2017; Southwood et al., 2004; Tallamy et al., 2021). This is especially true for lepidopteran larvae, which exhibit considerably lower survival rates on non-native compared to native host plants (Yoon & Read, 2016), even within the same plant genus (Burghardt et al., 2010). A recent study from Northern Europe further emphasizes the importance of plant origin (native vs. non-native): invertebrate abundance was much more reduced on non-native trees than urban trees (Jensen et al., 2022). Besides plant origin, leaf type can also impact arthropod abundance and therefore birds' breeding success, as leaf-feeding caterpillars are usually more abundant on broadleaved than on coniferous plants (Massa & Valvo, 1996).

Although previous studies reported associations between poor breeding success of urban birds and reduced vegetation cover (Corsini et al., 2020; de Satgé et al., 2019), most of such studies tended to focus on the amount of woody vegetation or the abundance of one or two tree species (e.g. Caizergues et al., 2018; Jarrett et al., 2020; Jensen et al., 2023), with detailed habitat surveys being rare (but see Mackenzie, 2010; Narango et al., 2017). Furthermore, in response to the scarcity of canopy-dwelling arthropods, city birds may also utilize alternative foraging substrates (e.g. shrubs and ground vegetation) and novel food sources (e.g. bird feeders) or expand their foraging areas. Yet, the reliance of breeding birds on alternative food sources to feed their offspring is seldom quantified in urban avian ecology (but see Catto et al., 2021; Cowie & Hinsley, 1988; Sinkovics et al., 2021). Therefore, it is important to consider the finer details of urban vegetation and the alternative foraging opportunities to improve our understanding of how insectivorous birds cope with food limitation when raising their chicks, and ultimately, how we can sustain wildlife-friendly green spaces in our cities.

With this overarching aim, we conducted a study using individually marked great tits, radio-telemetry tracking, real-time foraging observations, video recordings of nestlings' diet, and detailed plant surveys within the birds' territories in a Central-European city. Through these complementary methods, we aimed to establish direct links between breeding birds' habitat use, vegetation preferences, and nestlings' food composition, with three main objectives. First, we investigated the microhabitat use of parent birds, to describe general patterns of foraging distance, usage of bird feeders, and division of foraging time between different feeding substrates. Second, we used high-resolution spatiotemporal data on individual foraging trips to assess whether parent birds prefer native or non-native vegetation, broadleaved or coniferous plants, and to identify frequently visited or avoided plant species. Third, we examined how the various characteristics of individual plants influenced the birds'

foraging decisions (choosing plants to visit and allocation of searching time), foraging success (quantity and quality of food brought to the nest), and the time efficiency of parental food deliveries to the chicks.

Methods

Field methods

Study subject: In 2021, we monitored the nest boxes twice a week starting from late March to identify active great tit nests in the city of Veszprém, Hungary (see detailed description in chapter 2.2. *Study sites*). During the breeding monitoring, we mainly followed the field protocol, described in chapter 2.3. *General fieldwork*.

We selected eight focal nest boxes situated on bird territories that are representative of our urban study site (Appendix Figure S5.1, Table S5.1), and suitable for radio-telemetry tracking. These sites contained block housing areas, a university campus, a parking lot, an old cemetery, and urban parks that are heavily used by the public for recreation and other events. Due to logistic reasons, focal broods were distributed throughout the whole breeding season to facilitate fieldwork by avoiding synchrony between focal nests (hatching dates between April 29 and May 29; Appendix S5.1: Table S5.2).

On day 10 post-hatch (in one case on day 11; hatching day of the first chick = day 1) we trapped the female parent on the nest. Each bird received a unique combination of a numbered metal ring and three plastic color rings, for individual identification. We recorded the body mass (to the nearest 0.1 g), and used Rappole-harness (Rappole & Tipton, 1991) to equip females with a custom-made radio transmitter (transmitter dimensions: 10 x 5 x 4 mm; weight: 0.50 g, corresponding to an average of 2.91 % (range: 2.75–3.09) of the tagged birds' body mass). The whole handling procedure took ca. 10 mins (range: 6–13) after which we put the bird back on its nest. Unfortunately, one of the eight candidate broods failed 2 days after equipping the radio transmitter due to nest desertion and was thus excluded from further data collection. (This was a replacement brood and the latest of the involved broods.) The breeding biology parameters of the remaining seven focal broods are summarized in Appendix Table S5.2.

We re-captured five out of the seven focal females during subsequent breeding events (either in 2021 or 2022) and removed their expired transmitters (two birds lost the transmitters already). We did not observe any negative effects (e.g. skin irritation, unusually low body mass) on the re-captured birds. We only equipped female great tits with transmitters for three reasons. First, we confined our study to the second half of the chick-rearing period in each

nest to minimize the negative effects of trapping; however, during this period the male parent decreases its share in feeding the young (Kluijver, 2002). Second, our earlier research in the same study system revealed that males react more sensitively to being captured and ringed on the nest, and this can negatively affect both their nestling provisioning rates and the behaviour of their non-captured mates at the nest – even days after the disturbance (Seress et al., 2017). Third, extra-pair paternity is quite common in the studied urban great tit population (Pipoly et al., 2019), therefore males' habitat use and foraging behaviour can be confounded by forays to other territories for extra-pair mating or even chick-feeding at secondary females' nests.

Radio-telemetry tracking and field observations: After equipping females with the radio transmitters we left them to habituate for 1-2 days (mean = 33.5 ± 19.3 [SD] h). Then, we tracked each bird using a Yagi-antenna and a custom-made receiver that was communicating with a custom-developed smartphone application. The application visualized the received signal strength and the direction of the best-quality signals (during taking compass bearings) and was also continuously communicating with Google Maps. This system, with the 2-sec signal frequency, allowed us to quickly localize tagged birds and record the exact coordinates of their observed locations. The radio transmitters, the receiver, and the application were specifically developed and manufactured by Richárd Wohlfart research engineer, and his research team for this project (www.telemetry.hu). We had 4–7 tracking periods per brood when nestlings were 11–20 days old, and for each brood, we recorded a maximum of one tracking per day (62–130 min duration per tracking; mean = 92 ± 17 [SD]). The time of the day at the start of the radio tracking was between 9:00 and 11:00 for the majority of the tracking sessions ($n=27$) while the rest fell between 11:00 and 13:00 h ($n=15$). We did not record during strong wind or heavy rain.

At the beginning of each tracking session, Observer #1 (KS or BB) conducted a quick nest inspection to count the number of chicks and equip a small, hidden video camera to record parental food deliveries (detailed later). During this brief disturbance, Observer #1 was wearing a face mask and a hoodie for concealment. After leaving the vicinity of the nest and removing the hoodie and the mask, Observer #1 joined Observer #2 (GS) for the rest of the tracking session. This way we could reduce the chance of focal birds recognizing the observers and behaving agitated when these people appear around their nests (G. Seress, pers. obs.). Birds quickly resumed their normal activity after the disturbance and often allowed the observers to approach them as close as 5-10 meters during the tracking sessions, apparently without changing their normal behaviour.

During each tracking session, we combined radio-telemetry tracking with continuous field observations and synchronized voice recordings of researchers' notes on the focal bird's behaviour and habitat use (detailed below; Figure 1A). Observer #1 took compass bearings to search for the broad location of the focal bird, then continuously narrowed down its more exact location by the received signal strength. Meanwhile, Observer #2 was actively looking for the focal bird using binoculars (Nikon Monarch, 10×42). Once the focal female was spotted, we recorded its exact location (coordinates on Google Maps), its behaviour (see categories below), and the substrate type it was using (tree, shrub, vine, ground, in/on the nest box, building, or bird feeder). If the bird was spotted on a tree, shrub, or vine, we also noted the plant species used. The observation was continuous and we recorded every switch in the location, behaviour, substrate, or plant species until the bird was lost; we resumed the observations once the focal female was relocated. Given that females frequently returned to the nest to feed their young, in rare cases when we lost a bird's location, we could usually shortly resume the observations by returning to the nest and waiting for the female's subsequent appearance. To categorize behaviour, we considered an individual to 'forage' when we observed it actively searching for food (e.g. scanning the canopy, picking the leaves, moving along twigs or branches) or consuming a prey item. We categorized behaviour as 'other' if the female was preening, resting on a branch, soliciting the male, or perching with a food item (typically close to the nest box, before delivering prey to the nest); 'on nest' if the bird was inside the nest box (e.g. feeding or warming the chicks); 'alarm' if it was making alarm calls and/or behaving agitated (e.g. defending its territory against conspecifics or predators); 'fly' if the bird was flying between locations; 'unknown' if we did not have a view of the bird (e.g. it was in dense vegetation, or we lost its location).

Video-recording of parental provisioning: To link females' habitat use with the prey type delivered to the nest, we also video-recorded the nests throughout all tracking sessions. We used a small video camera (GoPro HD HERO3 or SjCam SJ4000) hidden in a black plastic box outside the nest (c. 15 cm from the entrance hole) that is a constant part of our nest boxes (Seress et al., 2017). From the videos, we determined the sex of the parent and prey type, categorized as 'caterpillar', 'other arthropod' (e.g. spiders, moths, *Physokermes* scale insects), or 'plant' food item (e.g. fruits, walnut, or sunflower seeds) for each parental visit. We categorized a prey item as 'unrecognizable' if it was not identifiable from the video recording. For the analyses, we used only the feeding data of the females, and excluded events when the female entered the nest apparently without food (n=11 visits).

Plant surveys: Between July and September 2021, we conducted detailed vegetation surveys to quantify plant species' availability and relative abundance on the seven focal territories. We chose to survey a 60-m radius area around the focal nests because the majority of the focal birds' registered foraging locations were within 60 m (see Results), and also because further increments in the radius would have greatly increased the survey effort. Note that this 60-m radius corresponds to or is comparable with the area size used for characterizing habitat for breeding passerines in recent urban ecology studies (e.g. Caizergues et al., 2021; Jarrett et al., 2020; Narango et al., 2017). During these surveys, we focused on woody plants, rather than all plant species because the former constitute the majority of the plant biomass in our urban study area, and focal birds were mostly using these during the tracking sessions (pers. obs.). We identified and recorded the GPS coordinates of all trees that reached at least 15 cm trunk circumference at chest height, shrubs of at least 3 m of height, and patches of common ivy (*Hedera helix*) that reached at least 0.5 x 0.5 m. We also estimated the surveyed plants' canopy height to the nearest 0.5 m by eye (with the aid of a 3-m measuring stick placed against the trunk as a reference), and measured canopy width at the widest point and the width perpendicular to it (to the nearest 0.5 m). From this data we calculated the canopy volume for each plant surveyed, using either the elliptical cone, the elliptical cylinder, the ellipsoid, or the hemi-ellipsoid volume formula (i.e., the shape that best approximated the species' canopy shape). The advantage of this method is that it takes into account multi-level and overlapping vegetation layers, thus enabling a more precise estimate of the amount of available vegetation when compared to measurements taken on satellite images. Finally, we considered a species to be native if it has native spatial range in the Carpathian basin according to the Pannonian Database of Plant Traits (Sonkoly et al., 2023) and the European Atlas of Forest Tree Species (San-Miguel-Ayanz et al., 2016). In total, we surveyed n=1197 woody plants (n=927 trees, 129 shrubs, and 141 ivy patches) belonging to 89 plant species within the 60-m radius areas, and also registered n=112 plants and 6 further species that birds visited foraging at least once outside the 60-m radius. (Note that we did not measure canopy volume for these latter, and used these locations only in a subset of analyses; see sections 1 and 3.4 below). For more details on the vegetation surveys see Appendix Table S5.3 and Figure 5.1C).

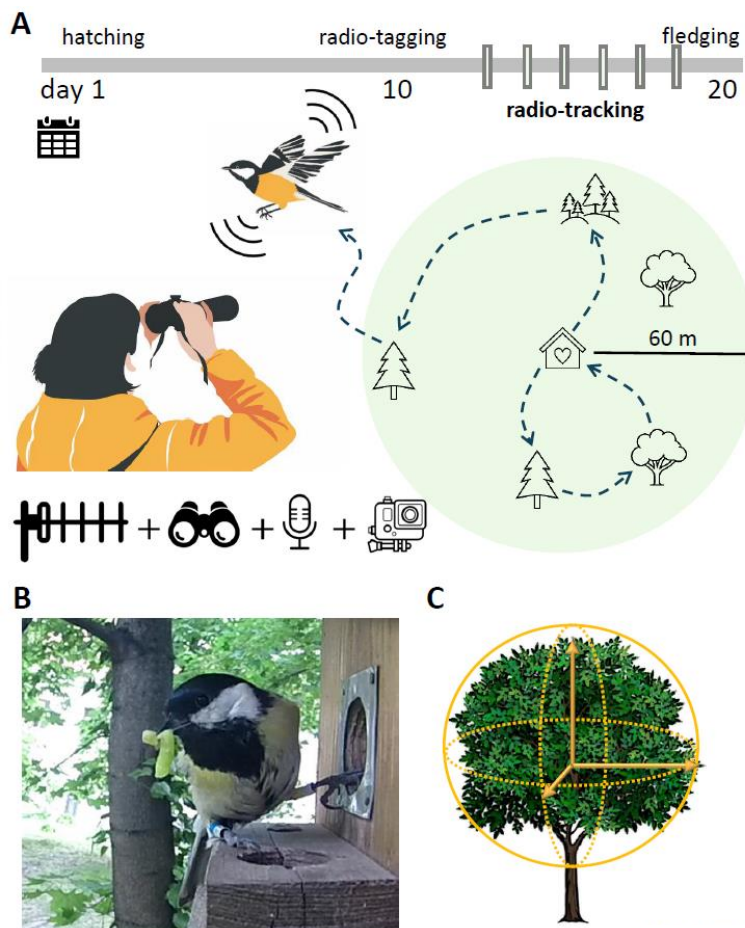


Figure 5.1. Infographics summarizing the main steps of the fieldwork. (a) We equipped urban great tits ($n=7$ females) with radio transmitters during the nestling-rearing period, then we tracked each bird through 4–7 tracking periods to record their habitat use (foraging locations, foraging substrates, plant species used); we combined radio-tracking with continuous field observations. (b) To link birds' habitat use with the prey type delivered to the nestlings, we video-recorded the focal broods throughout the tracking sessions. (c) We conducted detailed vegetation surveys to quantify plant species' availability and relative abundance around the focal nests. Image credits: (a) Veronika Bókony; (b) Gábor Seress.

Data processing & analyses

(1) Foraging distance and habitat use of foraging birds: The video recordings, the radio-telemetry tracking, and the voice recordings of researcher comments during the field observations were all synchronized. Thus, each behavioural event had a type (e.g. 'forage', 'on nest'; see above) and a starting and an ending time (hh:mm:ss), and the difference between these two times yielded the precise duration of the given behaviour (expressed in seconds). Since we also recorded the location of the focal birds and the plants on the territory, we used QGIS software (v. 3.32.2) to link each observed behavioural event to an exact location (GPS coordinates), substrate type (e.g. tree, shrub, ground; see above), and plant species (if the substrate type was 'tree' or 'shrub'). We did not include very short stopovers or flying bouts; these occur as 1-4 sec gaps in our dataset. This approach resulted in a behavioural and spatiotemporal dataset consisting of $n=3893$ behavioural events that we used for calculating descriptive statistics on the focal birds' detailed time budgets and habitat use.

(2) Plant preference of foraging birds: Separately for each territory, within the 60-m radius area of the focal bird's nest box, we calculated the female's relative foraging time (foraging time divided by total foraging time on plants) for each plant species and for each plant group (i.e. native, non-native, broadleaved, conifer, and the combinations of these categories). We applied chi-square tests ('goodness of fit') to test whether the distribution of relative foraging time spent on individual plant species or groups differs significantly from what would be expected based on the availability of plant species or groups (Narango et al., 2017). For this test, we expressed plant availability as the total canopy volume of the given plant species or group within the territory. Since our effort and success of radio-tracking varied between focal individuals (see Appendix Table S5.4), and the territories also differed in their plant species composition, we performed these analyses separately for each focal bird (territory). After each global chi-square test, we calculated p-values ("pairwise comparisons") for each plant species or group using the 'chisq.theo.multcomp' function of R package 'RVAideMemoire' (Herve, 2023) and applied the simultaneous Bonferroni method for correcting p-values for multiple comparisons.

To quantify the birds' foraging preferences, following Narango et al. (2017), we calculated the foraging preference index (FPI) for each plant species and group as the difference between the female's relative foraging time on it and the relative canopy volume of that plant species or group (i.e. total canopy volume of the given plant species or group within the territory divided by the total canopy volume of all plants within the territory). Positive FPI values indicate a preference and negative values express avoidance, while a close to zero FPI refers to birds using a plant species (group) as would be expected by chance. We used the FPI to visualize birds' foraging preferences and to rank plant species on each territory from the most preferred to the least preferred. Then, we calculated the average rank value for each species to identify the most and least preferred plant species across all birds.

(3) Individual plant characteristics affecting birds' foraging choices and behaviour: Here we used individual plant traits (of trees, shrubs, and ivy patches) and birds' foraging data (foraging time or prey items delivered to the nest) from the 60-m radius area of the focal bird's nest box. We used generalized linear mixed-effects models with spatial autocorrelation, implemented in the R package 'spaMM' version 4.1.20. (Rousset and Ferdy 2014). We fitted separate models to test our specific questions (detailed below) and included the following plant traits as numeric predictor variables: canopy volume of the individual plant (m³) – as bigger canopies host more invertebrates thus potentially being more attractive for foraging birds; total canopy volume of the plant species (m³) – as availability of a plant host species is

expected to positively affect the arthropod populations feeding on them; distance from the nest box (m) – as chick-feeding parents may prefer plants that are closer to the nest box. All numeric predictor variables were centered to the median before analysis. As categorical predictor variables, we included plant origin (native/non-native) and leaf type (broadleaved/conifer). Initially, we also included the plant origin x leaf type interaction; however, this term was non-significant in all models ($p > 0.199$), so we excluded it from the results presented here to facilitate the interpretation of the main effects. Multi-collinearity among the predictor variables was negligible as indicated by low values of the variance inflation factor ($VIF < 1.4$) in all cases.

All these models included data from all seven focal territories, so we used nest box identity as a random intercept term to control for the non-independence of the data from the same territory. Also, to control for the difference in sampling effort (as the number of tracking sessions and the success of radio-tracking differed between focal birds), each model contained an offset variable (detailed below for each model). We also tested the effect of spatial autocorrelation in all cases because we expected that the chance for a bird to forage on a given plant is increased if it is close to a plant the bird is currently using. We used the Matérn correlation structure with different correlation parameters allowed for each territory. We checked the validity of statistical assumptions for each model by residual diagnostic plots, as well as the significance of spatial autocorrelation by Moran's I test on the residuals, using R package 'DHARMa' version 0.3.4. (Hartig, 2019). All analyses were conducted in R (v. 4.2.1, R Core Team). With this general modelling framework, we tested the following specific questions.

3.1. Which plant traits influence the individual plant choice of foraging birds? Here we performed a two-step analysis. First, we built a model with beta-binomial error distribution, in which the dependent variable was whether the focal bird used or not used the individual plant for foraging at least once. In the second model, we included only those plants on which the female foraged at least once, and the dependent variable was the time spent foraging (in sec) with a gamma error distribution and log link function. As an offset variable, we used the total time spent foraging on plants (calculated for each focal bird separately) in both models (the offset variable was log-transformed for models where we used a log link function). Note that these analyses included all observed foraging behavior, i.e. the females could have foraged for themselves or for their chicks (as it was impossible to observe exactly when and how many prey items the birds consumed during foraging).

3.2. Which plant traits influence the amount and type of arthropod prey brought back to the nest? The vegetation preference of parent birds may not be the same when foraging for themselves or searching for food for their chicks, as not all food items are brought back to the nest. To analyse food deliveries to nestlings in relation to individual plant traits, we built two models. In the first model, with negative binomial error distribution, the dependent variable was the total number of prey items (caterpillars, other arthropods, and unrecognizable prey items) that the focal female brought back to the nest from the given plant. It is very likely that unrecognizable prey items in this dataset did not contain non-arthropod (i.e., plant-type) food items, for two reasons. First, we included only the deliveries from trees, shrubs, and ivy patches in this model, whereas focal birds collected plant-type food (e.g. sunflower seeds, walnuts) from the ground or bird feeders, with the sole exception of black mulberry (*Morus nigra*) fruits – but these fruits were very conspicuous on the video recordings and this plant species was present within the 60-m radius area in only one territory. Second, only prey items whose collection location was known were included in this model, and – apart from the black mulberry and the cherry plum (*Prunus cerasifera*) – we are not aware of any surveyed plant species (that birds visited) that bore fruits during the period of telemetry tracking.

In the second model, with binomial error distribution, the dependent variable was the proportion of caterpillar prey (as one of the most important food sources for tit nestlings – see the Introduction), i.e. the number of caterpillars brought from the plant divided by the sum of caterpillars and other arthropods brought from the plant. Note that here we excluded unrecognizable food items as these could also have been caterpillars. As an offset variable, we used the total time spent foraging on plants (calculated for each focal bird separately) in both models.

3.3. Which plant traits influence the time efficiency of parental food deliveries? To express the efficiency of finding food, i.e. the number of prey collected per unit of time, we analysed the number of prey items brought back to the nest from a plant relative to the time spent on that plant. In this model, we used negative binomial error distribution, the dependent variable was the total number of prey items (caterpillars, other arthropods, and unrecognizable prey items) delivered back to the nest, and the offset variable was the total amount of time (sec) spent foraging; we calculated both variables for each individual plant for each focal bird.

3.4. Which are the most profitable locations for collecting chick food? To compare plant species as well as other feeding substrates in terms of their profitability, we considered two aspects: time efficiency and food quality. To do this, we used all locations that were visited by the foraging focal female at least once (i.e. including plants farther than 60 m from the nest

box, as well as bird feeders and ground locations). To express the efficiency of collecting food, as above, we fitted a negative binomial model in which the dependent variable was the total number of prey items delivered back to the nest from the given location (including locations the bird foraged on but did not deliver prey from), and the offset variable was the total time spent foraging at that location (excluding locations that the female never visited during tracking). The only covariate was the location's distance from the nest, and besides the territory identity (nest box ID) random factor, we also included substrate species identity as another random factor. Substrate species identity for non-plant locations was either "ground" or "feeder". From this model, we calculated time efficiency scores as the random intercept values for each plant species, the ground, and bird feeders.

To express food quality, we used the same dataset as for calculating foraging efficiency scores, but we restricted it to those locations where at least one recognizable prey item was delivered to the nest. The dependent variable was the proportion of caterpillars out of all recognizable prey items (including other arthropods and plant-based food items), and this model had beta-binomial error. As above, the only covariate was the location's distance from the nest, and there were two random factors: territory identity (nest box ID) and substrate species identity. From this model, we calculated the caterpillar score as a measure of food quality by extracting the random intercept values for each plant species, the ground, and feeders.

Thus, these two scores estimate the two aspects of profitability for each substrate species, averaged across all territories. To test the correlation between these two aspects, we used a weighted Spearman correlation test, in which the weight variable was the number of locations belonging to the given substrate species (i.e. each plant species, ground, feeder) where at least one recognizable prey item was delivered to the nest in the whole dataset. Finally, we ranked all substrates along the two aspects of profitability to assess which plant species (or other substrate types) were the best foraging sites for urban birds.

Results

(1) Foraging distance and habitat use of foraging birds

We extracted behavioural data from 42 tracking sessions, totalling 65 hours and 22 minutes. To characterize focal females' territory use during foraging, we used every observation with behaviour type 'forage' when both the substrate type and the female's exact location were known ($n=1337$ foraging observations, 29h 13 min in total). Among the recorded behaviour types, radio-tracked females spent most of their time foraging (median: 44.6%, range: 36–59.8%), and instances where the behaviour or location of a bird was uncertain accounted for 26.7% (19.6–35.1%) of focal birds' time budget (Appendix Table S5.4). The time spent on each behaviour type is summarized separately for each focal bird in Appendix Table S5.4. Foraging females used tree canopies most frequently (Figure 5.2), accounting for 76.2% (median) of their foraging time (range: 16–92.2%). More than one-quarter of the foraging time was recorded on other substrates: ground (mostly covered with thin herbaceous layer, but sometimes bare surfaces; 13.1%, 0.6–27.9%), bird feeders (7%; 0–39.3%), shrubs (4.4%, 0.2–15.7%), vines (predominantly patches of common ivy; 2%, 0–34.5%), and very rarely buildings (0%, 0–0.2%).

Females were foraging most of their time within the 60 m radius of the nest (median: 64.9%; range: 53.7–89.9%) but also visited locations at 60–120 m relatively frequently (25.1%; 2.6–46.3%; Figure 5.3A). Occasionally, three out of the seven focal birds flew beyond 120 m in searching for food; these foraging bouts constituted 15.6% (11.2–21.3%) of these three birds' foraging time budget. The most frequently visited foraging substrates (trees, ground, shrubs, and feeders) were used across all distances from the nest, with one notable exception: feeders were used only at relatively large distances from the nest (Figure 5.3B). During the study we registered a total of 7 active feeders (1–2 per female) that were visited by five out of the seven focal females at least once; these feeders were located ≥ 49 m from their nests. The two longest distances at which we registered foraging were at 303 and 379 m distance from the nest; both locations were bird feeders.

From the video recordings, we registered $n=631$ female-delivered food items distributed between prey type categories as follows: caterpillars 19.4% (median; range: 0–46.2%), other arthropods 42.4% (5.5–70%), and plant-type food 9% (0–51.6%); while 23.1% (4–42.9%) of the food items delivered to the nestlings were unrecognizable.

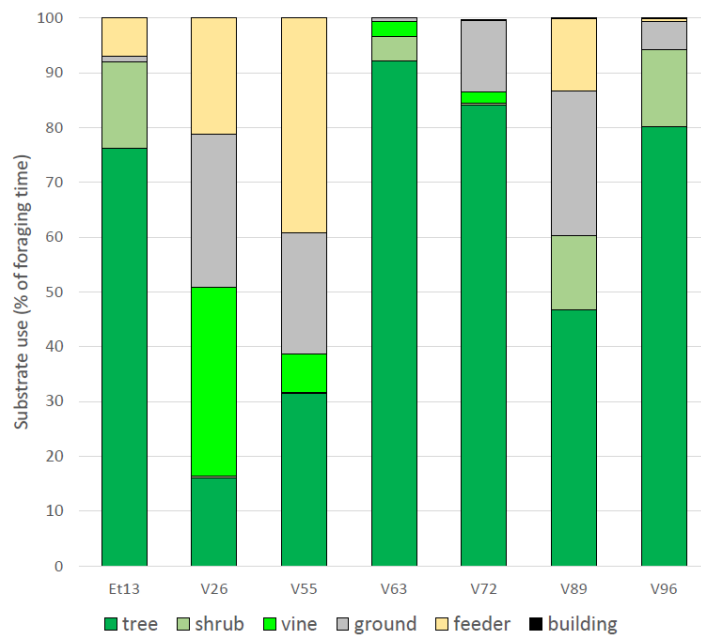


Figure 5.2. Percentage of foraging time on each substrate type by each great tit female (n=7). The numbers below the columns are the unique identifiers of the focal birds corresponding to Appendix Figure S5.1.

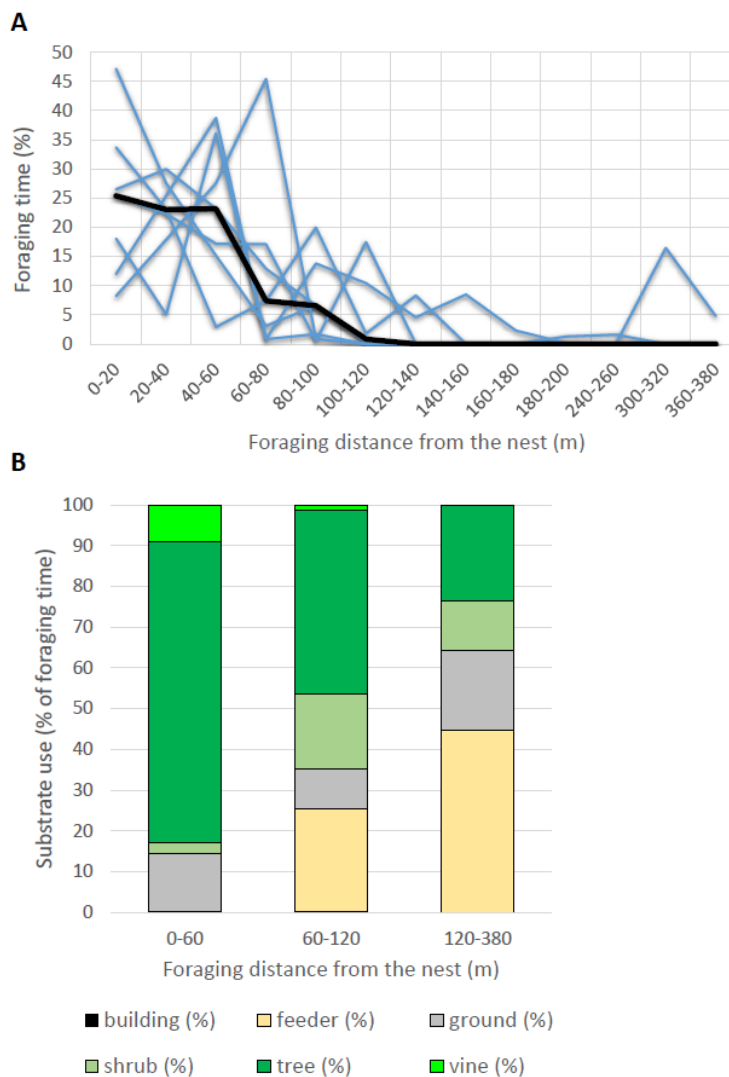


Figure 5.3. (a) The distribution of the percentage of total tracking time spent foraging by great tit females in relation to foraging distance from the nest. For illustration purposes, we pooled foraging data for every 20-m interval. Blue lines represent the individual birds and the black line shows the median of the seven females. **(b)** The distribution of the percentage of foraging time on each substrate type in relation to females' foraging distance from the nest. For illustration purposes, we pooled the data for three categories (0–60 m, 60–120 m, and >120 m). Note that buildings within 0–60 m and 60–120 m, and feeders within 0–60 m were used <0.5 % of time, so their share is not visible in these bar plots.

(2) Plant preference of foraging birds

When focusing on plant groups, we found that every female showed significant preferences by both origin and leaf type ($p < 0.001$; Appendix Table S5.5A). In 5 out of the 7 territories, great tits preferred native plants, while the remaining two birds preferred non-native vegetation (Appendix Figure S5.2). On the other hand, 3 out of 7 birds showed weak but significant preference (expressed by FPI) for broadleaved plants, while conifers were strongly preferred on the remaining 4 territories (Appendix Figure S5.2). When combining plant origin and leaf type, the chi-square tests again revealed significant differences in foraging preferences between these groups by all females (Appendix Table S5.5B) although this varied between territories. As a general pattern, birds strongly avoided non-native broadleaved plants on 6 out of 7 territories (Figure 5.4).

The distribution of time spent foraging on plant species was significantly different from the distribution of canopy volume across plant species on each territory ($p < 0.001$ in all focal birds), i.e. focal birds did not use the plant species according to their availability. In Background Data, we provide the list of plant species with data on their average FPI rank values, and the number of territories on which they were present, preferred, and avoided by foraging birds according to the results of chi-square tests. Among the most common plant species (i.e., present on at least 4 out of 7 territories) the ones with the highest average FPI rank value were the common ivy (*Hedera helix*), the cherry plum (*Prunus cerasifera*), the hedge maple (*Acer campestre*), the European spruce (*Picea abies*), and the common lilac (*Syringa vulgaris*); while the plants with the lowest average FPI rank value were the London planetree (*Platanus* sp.), the European ash (*Fraxinus excelsior*), the common hackberry (*Celtis occidentalis*), the Turkish hazelnut (*Corylus colurna*), and the European horse-chestnut (*Aesculus hippocastanum*). The amount of time spent foraging on individual trees is visualized on satellite maps separately for each focal female in Appendix Figure S5.3.

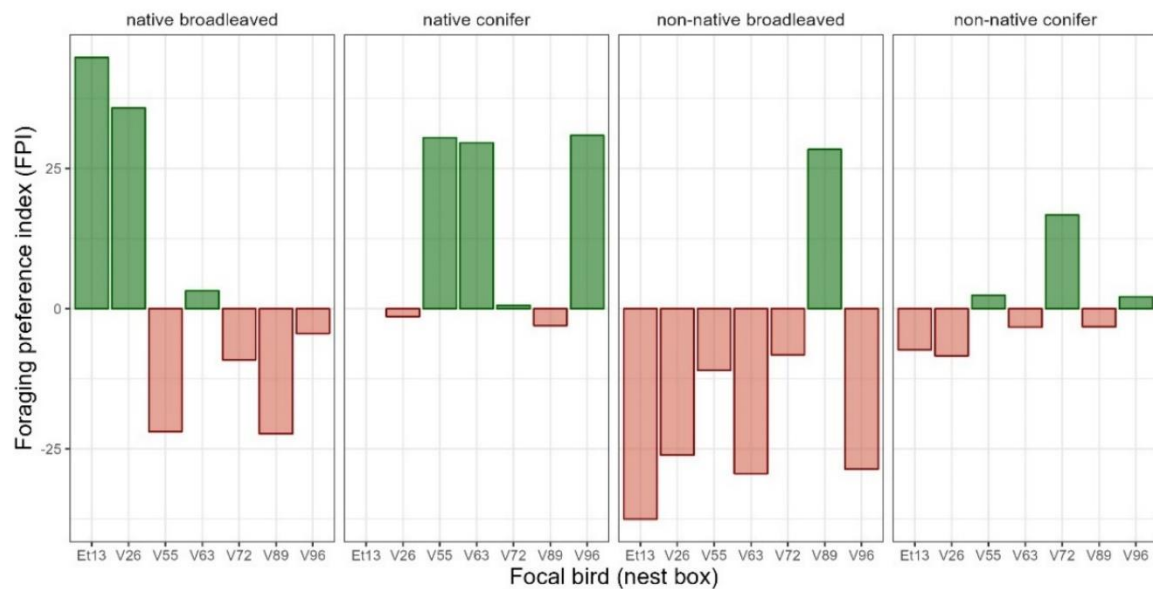


Figure 5.4. Great tit females' foraging preference or avoidance according to plant origin and leaf type in each territory. The foraging preference index (FPI) is expressed as birds' relative foraging time (%) spent on a plant group minus the relative canopy volume (%) of that plant group on a territory. Positive FPI expresses preference and negative values indicate avoidance, whereas close to zero values show that foraging frequency on these plant species was according to their availability on birds' territories. Note that on one of the 60-m radius territories (Et13), there were no native conifers.

(3) Individual plant characteristics affecting birds' foraging choices and behaviour

3.1. Which plant traits influence the individual plant choice of foraging birds? We found that foraging birds more often chose to visit individual plants that were native, closer to the nest, and had larger canopy (Table 5.1A). Among plant individuals that focal birds visited at least once, the time spent foraging was significantly and positively influenced by its nativeness and canopy volume, and negatively by the total canopy volume of the given plant species on the territory (Table 5.1B). Spatial autocorrelation was strongly significant in both models ($p < 0.001$), indicating that foraging birds visited a plant with higher probability and for longer periods of time if it was close to a plant that was also visited and used for a longer time, respectively.

3.2. Which plant traits influence the amount and type of arthropod prey brought back to the nest? Birds delivered more prey items to the nest from plants that were native, coniferous, closer to the nest, and had smaller total canopy volume on the territory (Table 5.1C). Canopy volume of the individual plant had a positive effect on the number of parental food deliveries; which did not reach but was close to statistical significance ($p = 0.056$; Table 5.1C). The proportion of caterpillars within the arthropod prey brought back to the nest was significantly lower for coniferous than for broadleaved plants; it was not significantly related to nativeness,

distance from the nest, individual canopy volume, and total canopy volume (Table 5.1D). There was no significant spatial autocorrelation ($p \geq 0.229$) in either model.

3.3. Which plant traits influence the time efficiency of parental food deliveries? By analysing the number of all prey items delivered back to the nest relative to the time spent searching we found that birds' efficiency was significantly higher on coniferous than on broadleaved plants (Table 5.1E). Nativeness, distance from the nest, individual canopy volume, and total canopy volume had no significant effect on time efficiency (Table 5.1E), and the spatial autocorrelation was also not significant ($p = 0.729$).

3.4. Which are the most profitable locations for collecting chick food? For foraging, the seven females used 64 plant species at 390 locations, 7 bird feeders, and 90 ground locations. We calculated time efficiency scores for these feeding sites. Further, we also ranked the proportion of caterpillars brought back to the nest across 34 plant species (98 locations), the ground (16 locations), and bird feeders (3 locations) from which a recognizable nestling food item was collected at least once. In the latter sample, we found a significant negative correlation between the time efficiency of collecting nestling food and the proportion of caterpillars brought back to the nest ($r = -0.434$, $p = 0.008$), indicating that the most time-efficient foraging spots yielded relatively few caterpillars. The efficiency scores revealed that bird feeders were by far the most time-efficient feeding locations in terms of the number of delivered food items per unit searching time at a given distance from the nest (Figure 5.5), followed mostly by coniferous plant species (e.g. Colorado spruce *Picea pungens*, European spruce *Picea abies*) and the sycamore maple (*Acer pseudoplatanus*). However, these species offered low food quality in terms of the proportion of caterpillars among the prey collected on them (Appendix Figure S5.5).

Table 5.1: Results of the generalized linear mixed-effects models testing the effects of individual plant traits on urban great tit females' foraging behavior. Dependent variables: **(A)** The selection (yes/no) of a plant to forage at least once; **(B)** the amount of time spent foraging on a plant (only plants that were used for foraging were included); **(C)** the number of arthropod prey items brought back to the nest; **(D)** the proportion of caterpillar prey (caterpillars/all arthropods) brought back to the nest; **(E)** the time efficiency of parental food deliveries (the number of prey items collected from a plant relative to the time spent on that plant). The parameter "plant origin" refers to non-native compared to native (intercept), "leaf type" refers to coniferous compared to broadleaved (intercept). Statistically significant ($p < 0.05$) differences from zero are highlighted in bold; those with $0.05 < p < 0.10$ are in italics.

Model coefficients	Estimate $\pm$ SE	t	P
(A) Plants chosen for foraging (yes/no) ¹			
<i>Intercept</i>	-10.53000 $\pm$ 0.22260	-47.30000	< 0.001
<i>Canopy volume (individual plant)</i>	0.00185 $\pm$ 0.00035	5.370000	< 0.001
<i>Canopy volume (total)</i>	-0.00002 $\pm$ 0.00003	-0.67500	0.49980
<i>Distance from the nest</i>	-0.03679 $\pm$ 0.00659	-5.57900	< 0.001
<i>Plant origin</i>	-0.54840 $\pm$ 0.18450	-2.97300	0.00301
<i>Leaf type</i>	0.32400 $\pm$ 0.23150	1.40000	0.16190
(B) Time spent foraging on a plant ²			
<i>Intercept</i>	-4.01062 $\pm$ 0.20270	-19.78300	< 0.001
<i>Canopy volume (individual plant)</i>	0.00069 $\pm$ 0.00018	3.76500	< 0.001
<i>Canopy volume (total)</i>	-0.00017 $\pm$ 0.00003	-6.61400	< 0.001
<i>Distance from the nest</i>	-0.00837 $\pm$ 0.00476	-1.75900	0.07983
<i>Plant origin</i>	-0.91469 $\pm$ 0.15700	-5.82500	< 0.001
<i>Leaf type</i>	0.20249 $\pm$ 0.19490	1.03900	0.29990
(C) Number of prey items collected ²			
<i>Intercept</i>	-9.39609 $\pm$ 0.22530	-41.70600	< 0.001
<i>Canopy volume (individual plant)</i>	0.00088 $\pm$ 0.00046	1.91700	0.05630
<i>Canopy volume (total)</i>	-0.00031 $\pm$ 0.00007	-4.19000	< 0.001
<i>Distance from the nest</i>	-0.02706 $\pm$ 0.00814	-3.32500	0.00101
<i>Plant origin</i>	-0.73607 $\pm$ 0.28150	-2.61500	0.00943
<i>Leaf type</i>	1.06162 $\pm$ 0.31760	3.34200	0.00095
(D) Proportion of caterpillar prey collected ¹			
<i>Intercept</i>	-10.1600 $\pm$ 0.63871	-15.90320	< 0.001
<i>Canopy volume (individual plant)</i>	0.00028 $\pm$ 0.00098	0.28960	0.77296
<i>Canopy volume (total)</i>	0.00008 $\pm$ 0.00014	0.53100	0.59706
<i>Distance from the nest</i>	-0.01542 $\pm$ 0.01411	-1.09230	0.27835
<i>Plant origin ¹</i>	-0.33330 $\pm$ 0.59701	-0.55820	0.57841
<i>Leaf type ²</i>	-3.78100 $\pm$ 1.12622	-3.35730	0.00126
(E) Time efficiency of parental food deliveries ²			
<i>Intercept</i>	-5.84200 $\pm$ 0.14800	-39.47775	< 0.001
<i>Canopy volume (individual plant)</i>	-0.00003 $\pm$ 0.00028	-0.09779	0.92218
<i>Canopy volume (total)</i>	-0.00004 $\pm$ 0.00005	-0.72787	0.46733
<i>Distance from the nest</i>	-0.00362 $\pm$ 0.00533	-0.67811	0.49829
<i>Plant origin ¹</i>	0.21900 $\pm$ 0.18300	1.19663	0.23252
<i>Leaf type ²</i>	0.77610 $\pm$ 0.19740	3.93229	< 0.001

¹ Estimates are on the logit scale; ² Estimates are on the log scale.

Discussion

In this in-depth study, we combined radio-telemetry tracking and real-time behavioural observations with detailed plant surveys and video recordings of nestlings' diet to better understand how urban breeding birds cope with food limitation. This comprehensive methodology enabled the collection of precise behavioural and habitat-use data and effectively reduced the possible bias resulting from the difficulty of detecting focal birds e.g. in dense vegetation or at the top of tall trees. To our knowledge, this approach resulted in one of the most detailed datasets available to date on the foraging patterns of urban breeding birds in a food-limited environment. To summarize our findings, we detected diverse territory-use patterns in urban great tits and confirmed that birds traverse great distances from the nest – often to visit bird feeders. We found that birds did not use the vegetation of the territory according to the relative availability of plant groups and species; instead, they generally avoided non-native plants when foraging. Plants with larger canopies and closer to the nest were used more, and birds spent less foraging time on plants that were more abundant (had higher total canopy volume) in the territory. We also found that somewhat different plant species emerged as 'the best' when we analysed birds' foraging time or considered only foraging locations from where parents collected nestling food. Moreover, there was a trade-off between the time efficiency of parental food deliveries and the quality of nestling food (i.e., the ratio of caterpillars): birds needed less time for collecting nestling food on conifers but these plants yielded less caterpillar prey compared to broadleaved vegetation.

Although our labor-intensive approach limited the number of females we could include in this study, we believe our findings can be generalized to some extent because we conducted repeated surveys for each bird, included focal broods from the entire breeding season (first and second clutches), and selected focal territories in a way to encompass a wide range of habitat diversity within the urban matrix (Appendix Figure S5.1). However, as our study was conducted in a middle-size city in Hungary, Central Europe, these findings should be generalized with caution to other geographical regions due to differences in local climate, floral composition, and arthropod fauna. Additionally, our study was restricted to female great tits, and there might be sex differences in habitat use, foraging strategies, or prey type composition. The literature suggests considerable variation in these aspects. For example, in forest habitats, male and female great tits have been reported to bring either similar (Pagani-Núñez & Senar, 2013) or slightly different composition of nestling food, while such effect was not present in the closely related blue tits in the same study region (García-Navas et al., 2013), nor in urban great tits (Senar et al., 2021) or house sparrows breeding in urban areas

(Seress, 2014). In a recent study that used a similarly small sample size as we did, radio-tagged urban male and female blue tits provided similar diets to their nestlings, yet male parents travelled somewhat further from the nest (Jarrett et al., 2020). To obtain a more comprehensive understanding of urban birds' habitat use, future investigations should include both male and female parents.

When assessing habitat quality for urban breeding passerines, there is a considerable variation in the size of the surveyed area, ranging from 100 m radius around the nest (Caizergues et al., 2018; Corsini et al., 2020) to 50 m (Caizergues et al., 2021; Narango et al., 2017), or even 35 m (Jensen, Ekroos, et al., 2023; Jensen, Ziegler, et al., 2023). However, most of the available information on foraging area size comes from optimal woodland habitats where parents collect the predominant proportion of nestling food from within 27–45 m (Hinde, 1953; B. Naef-Daenzer & Keller, 1999; Smith & Sweatman, 1974; Tremblay et al., 2005) or even 65 m (Krebs, 1971). These foraging area sizes may not fully apply to urban areas, as territory size heavily depends on habitat quality (Stauss et al., 2005). In response to the vegetation cover in cities, urban breeding great tits are expected to adjust their foraging behaviour by expanding their foraging range or utilizing foraging substrates other than tree canopies (i.e., their preferred foraging substrate in their natural woodland habitats). We found support for both. While our urban birds foraged mostly within 60 m of the nest (Figure 5.3A) and delivered more nestling food from plants that were closer to the nest, an intriguing finding was that they spent 35.1% of their foraging time beyond this distance (median; range: 10.1–46.3%). Other studies utilizing radio-telemetry in parid species reported that, in an urban park, 24% of the birds' foraging trips exceeded 50 m (Jarrett et al., 2020), while in an evergreen oak forest, considered as poor breeding habitat, this figure was 30% (Tremblay et al., 2005). Similarly, great tit territories in hedgerow habitats were found to be much larger albeit with significantly smaller amount of canopy compared to the nearby optimal woodland areas (Krebs, 1971). Although these studies used slightly different methodology and less precise estimates of birds' position and behaviour, their results agree with our findings, suggesting that urban parid species have larger foraging ranges compared to their conspecifics breeding in more favourable habitats. Therefore, we propose that studies assessing foraging area quality in urban breeding parids should consider an area with a radius of at least 60 m, because smaller-scale surveys might not provide reliable results.

Notably, in our study, the two out of the seven females that were not observed using bird feeders spent the majority of their foraging time (79.7% and 89.9%) within 60 m of the nest. On the contrary, the other five females were observed making frequent foraging trips beyond

60 m of the nest, often visiting bird feeders to gather food for their nestlings or to forage on the feeders themselves, sometimes flying as far as 380 m from the nest. These females spent at least 23.8% and up to 46.3% of their foraging time on feeders, even though feeders comprised only a tiny proportion of food sources available to the birds (i.e. we recorded 7 feeders as opposed to 335 trees visited at least once). These findings suggest that these anthropogenic food sources are highly attractive to nestling-rearing parents, probably because they offer a consistent and easily accessible food supply. Indeed, we found that the time efficiency of nestling food deliveries was higher from bird feeders than from any other plant species. Similarly, the foraging area use of urban house sparrows in the Czech Republic revealed that nestling-rearing parents flew the longest distances to reach trash bin locations and their foraging visit durations were also the shortest at these foraging spots (Havlíček et al., 2022). However, this convenience may come at a cost. Firstly, the nutritional composition of bird food (predominantly sunflower seeds in our region) is suboptimal compared to insect prey, potentially impacting the physiology of birds, especially nestlings (Catto et al., 2021; Seress & Liker, 2015). Secondly, the regular and prolonged absence of parent birds from the vicinity of the nest might compromise their ability to defend it from potential predators or competitors (Vafidis et al., 2018). Although we could not conduct a formal test of this hypothesis, an illustrative example was observed in a brood where the focal female often foraged on feeders more than 300 m away from the nest. During the survey period, a few chicks disappeared from the nest, most likely due to predation because we frequently observed a woodpecker on the nest box when the parents were not nearby.

In great tits breeding in their natural habitats, foraging upon the ground is observed more frequently outside of the chick-rearing period (Gibb, 1954). However, we found that our urban birds spent a non-negligible portion of foraging time (up to 28% per female) on the ground (Figure 5.2). This was unexpected, because the herbaceous layer is typically very thin and heavily mown, and the leaf litter is regularly collected and removed from beneath the trees, resulting in bare ground surfaces and sparse undergrowth in our study area. The observed foraging behaviour of great tits may be explained by the scarcity of natural prey items in their most preferred foraging locations, i.e. tree canopies (Seress et al., 2018). Additionally, urban habitat conditions often provide poor shelter for ground-dwelling arthropods and moth species whose larvae pupate at the ground level (Vergnes et al., 2014), which may reduce the searching time for birds feeding on them. However, ground locations in our study were unprofitable both in terms of the time efficiency of delivering food for nestlings and the proportion of caterpillars brought back to the nest (Figure 5.5). This result

suggests that the adult birds mostly visited ground locations to forage for themselves. When foraging on the ground, birds were persistently combing a patch (typically for minutes; mean=92±87 [SD] sec, n=156 cases), and often returned to the same spot at later foraging trips, suggesting that they expected to find food on the ground. Although we could not quantify the prey items consumed during these ground-foraging events, our field observations revealed that focal birds either scavenged upon cracked walnuts and sunflower seeds or were hunting for insects (e.g. turning over leaves).

Despite that non-native vegetation was abundant on the surveyed territories (42.8% of the estimated total canopy volume, and 60% of the surveyed plant species; Appendix S5.1: Table S5.3), foraging females showed a marked and general avoidance for these trees and shrubs, similar to former studies (Mackenzie et al., 2014; Narango et al., 2017). This pattern was especially prominent for non-native broadleaved species. One notable exception was a female in the territory with the lowest amount of canopy (V89) that exhibited strong preference for non-native broadleaves (Figure 5.4). This unexpected pattern, however, was mostly driven by two non-native plant species, the black walnut (*Juglans nigra*) and the black mulberry (*Morus nigra*). For both species, the visited specimens were within 20 m of the focal nest, and the time-efficiency of collecting nestling food (ripe fruits, in the case of the mulberry tree) was very high (Figure 5.5). This suggests that great tits' foraging choices (see above) and their general preference for arthropod prey items can sometimes be overridden by incidental circumstances that render certain non-native plants highly profitable sources of nestling food or water (i.e. juicy fruits).

We expected to find a general foraging preference for native broadleaved vegetation, yet our results revealed that birds' reliance on this plant group varied a lot between territories. For example, native deciduous oaks (*Quercus* sp.) are known to support rich arthropod communities (Southwood et al., 2004) and are generally preferred by foraging birds (Narango et al., 2017; Wood et al., 2012) including tits (Hino et al., 2002; but see Mackenzie et al., 2014). Therefore, the abundance of deciduous oaks is often used as an indicator of territory quality in urban bird studies (Caizergues et al., 2022; Jensen, Ziegler, et al., 2023; Mackenzie et al., 2014). In our study, we registered a total of three native *Quercus* species on four territories; however, focal females did not prefer oaks excepting a single territory. In this latter territory (Et13), there were relatively many oak trees, close to each other, whereas in the other territories, the oak specimens were scarce and scattered, surrounded by other, often non-native tree species. Such fragmented configuration may isolate individual trees, hindering the colonization and population growth of oak-dwelling arboreal insects (Mackenzie et al., 2014).

Therefore, we recommend considering not only the quantity but also the spatial arrangement of vegetation when assessing habitat quality based on vegetation composition.

Coniferous plants typically host poorer phytophagous insect fauna than deciduous species, due to their smaller leaf area and less palatable leaves (Basset, 1994). Therefore, it was unexpected in our study that when foraging birds showed avoidance, this was much stronger against broadleaved than coniferous plants, irrespective of the plants' native or non-native status. Notably, foraging great tits often preferred native conifers (Figure 5.4, Appendix S5.1: Table S5.5) despite that this group contributed only 3% to the estimated total canopy volume of the surveyed territories (Background Data). The most frequently visited conifer was the European spruce (*Picea abies*). Our field observations and video recordings revealed that birds predominantly collected *Physokermes* scale-insects from these trees (appearing as yellowish-brown globular 'lumps' in birds' beaks, as ovipositing female scale-insects become heavily swelled and amorphous). These arthropods are clumped and highly sedentary, and must have been present in great numbers on spruces (including the closely related Colorado spruce *Picea pungens* which was the most preferred species among the non-native conifers in our study) given that, upon discovering these insects, focal birds frequently returned to the same branch repeatedly, immediately after delivering their prey to the nest. This observation supports our result that, among all surveyed plants, focal birds were most efficient in collecting nestling food on conifers – especially on *Picea* species – despite that these plants yielded fewer caterpillars when compared to broadleaved vegetation. Additionally, during our field observations blue tits and coal tits (*Periparus ater*) also heavily utilized this food source, and were often seen foraging on the same spruce trees alongside our focal birds. Altogether, these findings suggest that the factors driving the foraging choices of urban birds are more nuanced than captured by the often-used simple categorizations of coniferous vs. broadleaved and native vs. non-native.

The availability of a plant host species (i.e., its total canopy volume in an area) is expected to positively influence the size of arthropod populations feeding on them, thus making them more attractive to insectivorous birds. Contrary to this expectation, we found that foraging birds preferred plants that were present with smaller total canopy volume on the territories, and spent less time foraging on and collected fewer prey items from the most abundant plant species. This result suggests that in our urban study site, the dominant tree species may not provide optimal foraging grounds for great tits. Despite constituting 50.5% of the estimated total canopy volume, the five most common tree species – each found across 4-7 territories – were significantly underused by foraging birds compared to their availability, as indicated by

these plants' low ranking by the average FPI (Background Data). These suboptimal tree species, listed from the highest to lowest average FPI rank, include the largeleaf linden (*Tilia platyphyllos*, native), the Norway maple (*Acer platanoides*, native), the European horse-chestnut (non-native), the European ash (native), and the London planetree (non-native). In Hungary, these tree species are all extensively planted in parks and along streets (Sonkoly et al., 2023), and many of them are also common in urban environments across Europe due to their aesthetic value or tolerance of stressful urban conditions (San-Miguel-Ayanz et al., 2016). The widespread use of these tree species in urban ecosystems raises the possibility that urban green spaces, not only in our study system but potentially beyond, may offer suboptimal feeding sites for insectivorous and canopy-feeding birds.

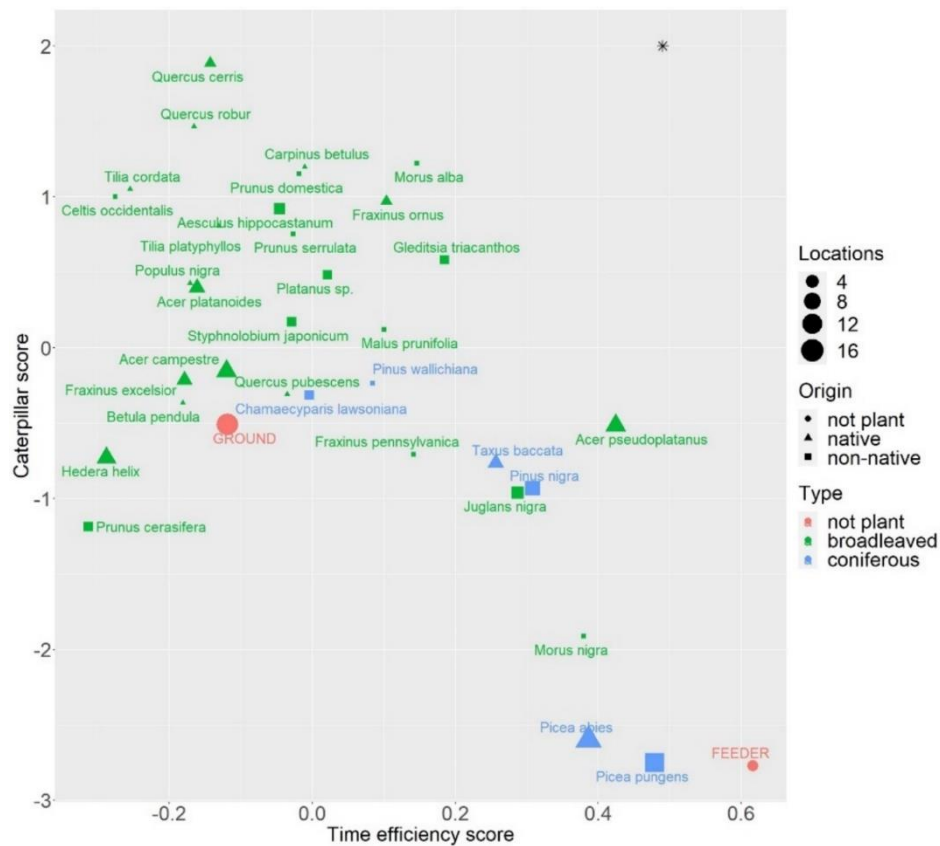


Figure 5.5. Plant species and other foraging locations (ground and bird feeders) along two aspects of profitability: time efficiency of finding food for nestlings and the proportion of caterpillars brought back to the nest. Symbol size is proportional to the number of locations where at least one recognizable prey item was collected. The asterisk marks the time-efficiency score of a native broadleaved species (*Sambucus nigra*) that was omitted from the graph to facilitate readability because it had an extreme caterpillar score (4.29) with very low weight (i.e. high estimation uncertainty, as only one out of the 13 available locations was used by a single female within a single tracking session). Note that this individual plant was not included in the analyses of plant traits because it was farther than 60 m from the nest.

On the other hand, the canopy volume of the individual plants had a positive impact on birds' foraging decisions. Birds visited large trees more often, spent more time foraging on and tended to collect more prey items from them. This finding corroborates former studies emphasizing that large urban trees are keystone structures in urban landscapes and their presence is strongly and positively associated with the diversity of herbivorous insects and birds (Campos et al., 2006; Stagoll et al., 2012 and references therein). Large trees provide diverse resources for wildlife, including dead wood, disproportionate amounts of leaves and flowers, cavities, etc. For example, Stagoll et al. (2012) found that in Australian parks adding five trees with >50 cm diameter at breast height increased avian species richness by ca. 10% but with >100 cm this effect was more than 150%. Unfortunately, such very large trees are rare in urban ecosystems (n=3 trees of the 896 surveyed trees in our study), therefore their preservation should be a priority in urban landscaping policies.

Conclusions

Our former studies in the same urban study system showed that food limitation during the breeding season plays a crucial role in urban great tits' decreased breeding success. This was clearly supported by an insect-food supplementation field experiment (Seress et al., 2020) and correlative results, such as the decreased amount of caterpillars in urban tree canopies (Seress et al., 2018) and in urban nestlings' diet when compared to nearby forest habitats (Sinkovics et al., 2021, 2023). Our current results complement these findings, revealing that urban great tits regularly travel large distances from their nests to visit bird feeders. While in food-limited environments bird tables undoubtedly offer a convenient solution for parents to address the energy demands of their growing chicks, the broader implications of this dependence – ranging from physiological effects to potential increases in predation risk (Hanmer et al., 2017) – warrant further investigation. As a general pattern, foraging birds preferred trees with large canopies, and avoided foraging on and feeding their nestlings from non-native vegetation. However, our results also highlight that if we aim to identify the most beneficial plants to create the best quality habitats for urban insectivorous birds, we need to consider multiple aspects. For example, the plant species or locations where great tits spent most time foraging (e.g. hedge maple, *Pinus* species, or ivy patches and ground locations) are not necessarily the same as from where they delivered the most food for their nestlings (e.g. *Pinus* species or the sycamore maple) and are definitely not the ones that offered the most caterpillars for the chicks (e.g. *Quercus* species). Therefore, while our study confirms that broad plant traits, like nativeness or leaf type, heavily influence birds' foraging decisions, it is

also evident that plants' contributions to local food webs can vary considerably even among species within the same category (Narango et al., 2020; Tallamy et al., 2021). This highlights the need for further research going beyond the native/non-native dichotomy to identify those plant species that play key roles in supporting robust ecosystems in urban settings. However, selecting the most suitable plant species for wildlife-friendly green spaces is challenging. Urban plants must not only be tolerant of the environmental conditions specific to cities and resilient to the predicted effects of climate change but they must also fulfil the well-being and aesthetic needs of human residents (Alizadeh & Hitchmough, 2019). Nevertheless, to make a good step in this direction, we advocate for the strategic planting of diverse, primarily native species and preserving large trees with extensive canopies. These measures are essential for creating and maintaining high-quality habitats for urban wildlife, particularly insectivorous birds.

6. Winter field survey of bird feeders in two Hungarian cities

Boglárka Bukor, Boróka Kósa, András Liker, Gábor Seress

This chapter is an extended version of the research article “Boglárka Bukor; Boróka Kósa; András Liker; Gábor Seress (2024) Winter field survey of bird feeders in two Hungarian cities. Ornis Hungarica, (1): 80–95.”

Introduction

The practice of bird feeding has emerged as a widespread and increasingly popular activity in human settlements, especially as more and more people are living in urban areas worldwide (Reynolds et al., 2017). This trend is reflected by the growing market for bird food production and sales (Orros & Fellowes, 2015; Plummer et al., 2019), establishing bird feeding as probably the most popular form of human-wildlife interactions (Baverstock et al., 2019; Jones & Reynolds, 2008). Typically, people provide food for birds not solely for welfare reasons or to aid conservation efforts, but also for aesthetic enjoyment, with many food-providing nature enthusiasts eager to discover the most preferred types of food to attract more birds to their bird tables (Cox & Gaston, 2015; Dayer et al., 2019; Galbraith et al., 2015). The practice of bird feeding is often encouraged by nature conservation organizations in many countries, particularly those in the Northern Hemisphere (Baverstock et al., 2019). This is not different in Hungary either, where urban residents commonly engage in bird feeding, especially during the winter months.

Considering the widespread occurrence of bird feeding, urban ecology studies generally recognize cities as more favourable habitats for many wintering birds compared to natural areas, primarily due to the increased availability of food sources during winter (Chamberlain et al., 2009; Evans et al., 2015; Robb et al., 2008). Beyond this, however, bird feeding has several further potential biological and ecological implications for feeder-visiting birds. Previous research on this topic has largely focused on how winter feeding influences avian community composition at feeding sites (Ferber et al., 2014; Galbraith et al., 2015; Pierret & Jiguet, 2018), health risks including pathogen exposure (Lawson et al., 2018; but see: Frątczak et al., 2021), mortality factors associated with feeding sites (Lawson et al., 2018; Robb et al., 2008; Tryjanowski et al., 2018), and occasionally the potential impacts of winter feeding on birds' physiology and reproductive success (Plummer et al., 2013, 2018). These

studies are very important by providing a more comprehensive understanding of the myriad effects of bird feeding on urban bird populations. However, many of these studies, being feeding experiments, may not necessarily provide insights into the prevalence and characteristics of local bird feeding practices. While there have been efforts to assess the extensive scale of bird feeding (Dayer et al., 2019; Horn & Johansen, 2013) or estimate bird feeder densities and the types of food provided at bird tables in urban environments (Orros & Fellowes, 2015; Plummer et al., 2019), actual field surveys and studies investigating human residents' bird feeding practices remain rare. Moreover, there is a notable gap in our understanding regarding the structural types and densities of bird feeders (Amrhein, 2014; but see: Tryjanowski, et al., 2015), factors critical in determining the number of bird species and individuals that can effectively utilize these resources. This is particularly true for regions beyond the USA and the UK (Baverstock et al., 2019; Reynolds et al., 2017), where bird feeding has been a longstanding tradition for decades and is studied most frequently (Cowie & Hinsley, 1988; Plummer et al., 2019). Therefore, while there has been a prevailing notion that in Europe bird feeding is far more prevalent in North-western European cities (Reynolds et al., 2017), research from Central and Eastern European countries is rare. From this region, to our knowledge, research published on human residents' bird feeding habits is only available from Poland where the authors found no significant difference in the number of bird feeders between urban and rural settings, although in cities a higher proportion of bird feeders were filled with food (Tryjanowski, Skórka, et al., 2015).

The aim of the present study was to provide an accurate picture of the prevalence of winter bird feeding in Hungary, Central Europe, in areas that considerably differ in their degree of urbanisation. Our study objectives were as follows. First, to survey the density and characteristics of winter bird feeders (placed by citizens) in Veszprém (a middle-sized city) and Budapest (the capital of Hungary) and also in nearby peri-urban forested areas with low housing densities. Second, to document the bird species and number of individuals attracted by the different types of feeders.

Methods

Study areas

We conducted our study in two Hungarian cities: Veszprém, a middle-sized city with ~57,100 residents, and Budapest, the capital city with 1,707,000 residents (Hungarian Central Statistical Office, 2021.01.01; https://www.ksh.hu/stadat_files/fol/hu/fol0014.html). For the winter bird feeder surveys, we selected five study sites in each city, comprising four urbanised areas (within the city) and one peri-urban wooded area in the proximity of the city (Figure 6.1). The survey areas were designated in those study areas where nest-boxes are located, which we also monitor during the breeding season.

A) City centre I (Veszprém): Located in one of Veszprém's central districts, this site surrounds the city's main bus station. It is a bustling area with several high-traffic roads, shops, offices, an urban park, and some residential buildings (47°05'46.3"N 17°54'45.6"E, area: ~0.12 km²).

B) Office area I (Veszprém): This site is located in the middle of the city near the main campus of the University of Pannonia. It features university buildings, parking lots, a nearby cemetery with mature trees, an urban park, office buildings, and high-traffic roads (47°05'19.1"N 17°54'34.3"E, area: ~0.333 km²).

C) Residential area I (Veszprém): The Egyetemváros neighbourhood is characterized by a mix of green spaces, recreational facilities, and residential buildings, including multi-storey block housing flats and houses with gardens. Another university campus with a large park is also located here (47°05'09.1"N 17°54'11.5"E, area: ~0.209 km²).

D) Residential area II (Veszprém): The Jeruzsálemhegy neighbourhood is primarily a housing estate with multi-story block housing flats, public green spaces, and an old and relatively undisturbed cemetery with mature broadleaved trees (47°05'36.8"N 17°53'51.2"E, area ~0.131 km²).

E) Office area II (Budapest): The Gesztenyés-kert park consists of green spaces, a shopping centre, and extensive office and sports facilities (47°29'22.8"N 19°01'14.1"E, area ~0.15 km²).

F) Urban park (Budapest): The Tabán urban park near the Danube River and adjacent to Gellért Hill's green area, is covered with large grassy fields, dotted with trees and bushes. It is a popular site for recreational activities among locals and it is surrounded by residential flats (47°29'33.9"N 19°02'16.7"E, area ~0.258 km²).

G) Residential area III (Budapest): Characterized mostly by residential multi-story blocks of flats and an urban park with green spaces and several recreational facilities (47°30'27.7"N 19°01'06.0"E, area ~0.299 km²).

H) City centre II (Budapest): This area features one of the main train stations of Budapest, and parking lots, office and residential buildings. A large urban park with green spaces and walking paths is also located here (47°30'03.7"N 19°01'37.1"E, area ~0.265 km²).

I) Peri-urban woodland I (Veszprém): The Gulya-domb is a semi-natural forest on the outskirts of Veszprém, adjacent to the zoo. This area is very popular for recreational activities with campfire spots and numerous hiking trails. The most common tree species are the native flowering ash (*Fraxinus ornus*), downy oak (*Quercus pubescens*) and Turkey oak (*Quercus cerris*), and the non-native black pine (*Pinus nigra*) (47°05'28.2"N 17°52'59.4"E, area ~0.292 km²).

J) Peri-urban woodland II (Budapest): The Ördög-orom within the borders of Budapest, is a semi-natural forest with weekend houses and hiking trails. This site is mainly characterized by the native common hornbeam (*Carpinus betulus*) mixed with sessile oak (*Quercus petraea*), English oak (*Quercus robur*) and flowering ash (47°29'09.6"N 18°58'42.2"E, area ~0.346 km²).

Field methods

We conducted bird feeder surveys during the winter season, between November 25, 2021 and March 1, 2022. Each site was surveyed three times with a minimum two-week interval between the consecutive surveys. Surveying took place only during favourable weather conditions (no snowfall or rain, wind force below 20 km/h [Beaufort-scale 3]) between 8:00 and 14:00. During these surveys, one or two observers equipped with binoculars walked through the study site at a slow pace, following a route that enabled to visually cover all accessible areas as much as possible without cross-passing. We meticulously mapped the location of every bird feeder and documented the following details: the type of the bird feeder (see below), the type(s) of food provided, and the abundance and species of birds visiting the feeders (detailed below).

We differentiated five types of feeders (following Tryjanowski, Skórka, et al., 2015): (1) typical bird table often with a roof (having a fixed position e.g. on a pole, fence, or window sill; (2) bottle-type hanging feeders providing seeds (often made from plastic water bottles); (3) fat balls; (4) food scattered on the ground (typically sunflower seeds, but sometimes

breadcrumbs or kitchen waste); and (5) mixed feeders where more than one feeder types were present together (e.g. bottle feeders with fat balls).

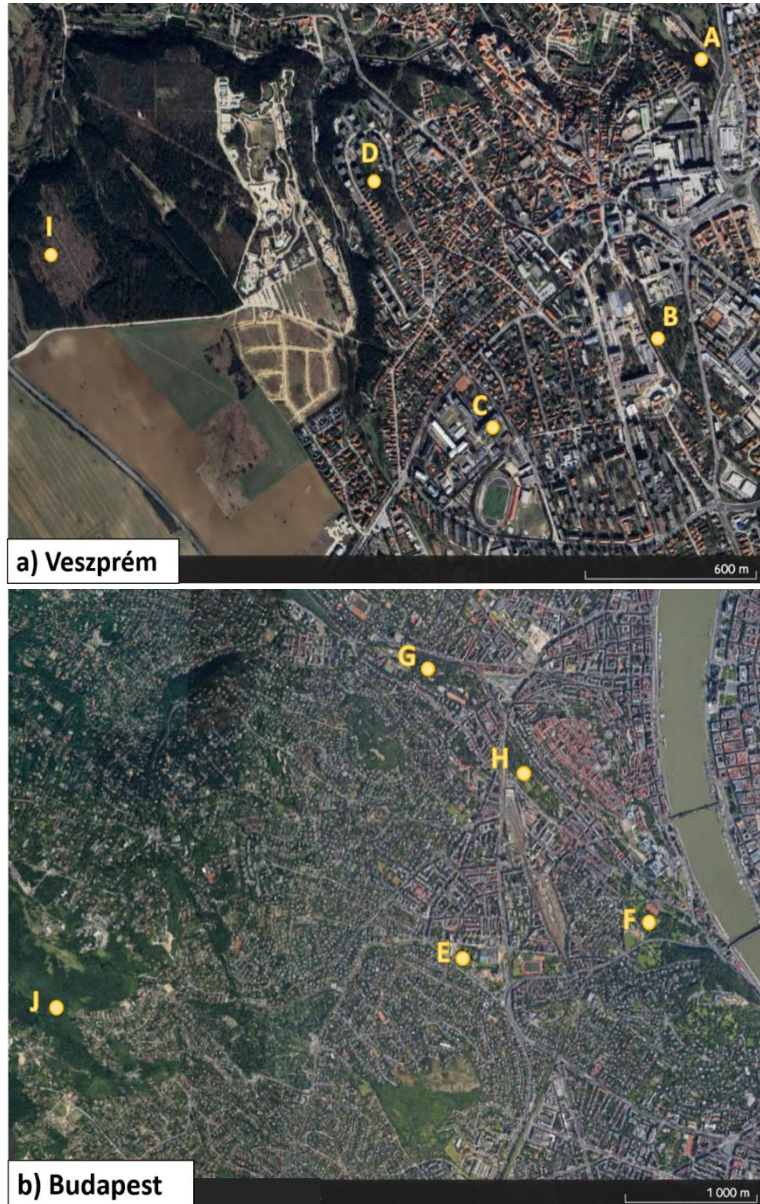


Figure 6.1. The map of the winter bird feeder survey sites in Veszprém (panel a) and Budapest (panel b) during the winter of 2021-22. A) City centre I; B) Office area I; C) Residential area I; D) Residential area II; E) Office area II; F) Urban park; G) Residential area III; H) City centre II; I) Peri-urban woodland I; J) Peri-urban woodland II.

Furthermore, we categorized the type of food provided at the feeders into seven main categories: (1) sunflower seeds; (2) seed mix; (3) fat ball (fat mixed with seeds); (4) animal fat; (5) nuts; (6) fruits; and (7) human food waste (e.g. bread, oat or cooked rice).

We also recorded the presence of birdbaths. Note however, that we started to record baths only during the first field surveys, and that due to the decreased visibility of baths, this type of

data was less accurate than the rest of the data collection protocol. Therefore, the data on the presence of birdbaths is likely incomplete to some degree.

During the surveys, we conducted observations at each feeder for 3–5 minutes (depending on the birds' activity on the feeder), to record all bird species appearing at the feeder. First, we recorded the number of species, estimated as the maximum number of bird species in one feeder per survey. Second, for each species present we also recorded the number of birds as the highest observed count of individuals that were present at the feeder and/or in its immediate vicinity during the observation period.

Statistical analysis

We analysed our data in RStudio (version 4.3.2.). For fitting generalized linear mixed models, we used Template Model Builder automatic differentiation engine (package 'glmmTMB' version: 1.1.7.; Brooks et al., 2017). We built generalized linear mixed models with Poisson distribution separately for the number of birds and the number of species (response variables). The models included feeder ID as a random factor. The models contained the following environmental predictor variables potentially affecting the number of birds and the number of species: feeder type (5 levels), the daily minimum temperature (on the day of the survey), the city (Budapest or Veszprém), the date (numeric variable; 1 = 25th of November, the date of the first survey), and the presence of a birdbath on the feeder (present/absent). Snow coverage (present/absent) was not included in the analysis, because snow cover was rare during the surveys and its presence was unbalanced between the study sites: snow coverage during survey days was present only in the two peri-urban sites and the urban sites in Veszprém, but never in the urban sites at Budapest. Removing step-wise the non-significant predictors from the models did not change the results qualitatively, so we present the results of the full models. We tested the fit of the models using the 'DHARMA' R package (Hartig, 2019); the fit of all models was acceptable. Finally, we compared the effect of the feeder type on the number of birds and number of species with Tukey's post-hoc tests (using R package "glht").

Results

Density of the surveyed feeders

We completed 30 surveys in total, three at each of the 10 study sites. During these, we mapped the locations of a total of 202 bird feeders that contained food on at least one occasion. The density of the active feeders (i.e. the feeders that contained food on a given field survey) varied highly across study sites and even from one survey to the next within the

same site, and was notably lower in the two peri-urban woodland sites compared to the other 8 urban locations (Table 6.1, Figure 6.2).

In the urban study sites in Veszprém, the number of active feeders varied between 11–33, translating to a density ranging from 60.1 to 206.1 bird feeders/ km². The feeder density was usually two times higher in Veszprém than in Budapest where, the number of active feeders ranged between 4–22, extrapolates to a density of 23.3–80.0 bird feeders/ km². At Veszprém, we found the highest feeder densities in the two residential areas (C and D), during all three surveys. But in Budapest, we found the highest feeder densities in the city centre area (H; Table 6.1, Figure 6.2). In comparison to the urban sites, bird feeders were much scarcer in the peri-urban forest sites in both cities. The number of active bird feeders ranged between 1–4 with their density spanning between 3.4–13.7 bird feeders/ km², in the peri-urban woodland at Veszprém (I). Similarly, in the peri-urban woodland at Budapest (J), the number of active feeders was 4–5, resulting in a density of 13.5–14.5 bird feeders/ km².

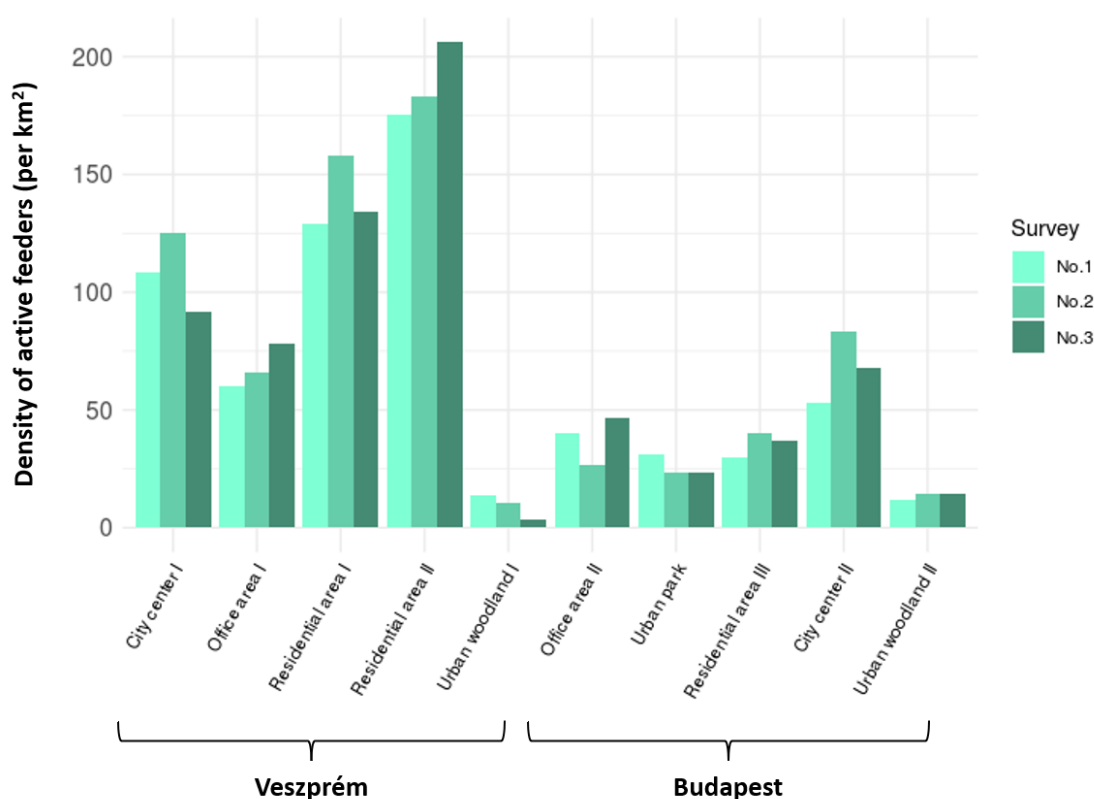


Figure 6.2. The density of active feeders at our four urban sites, and at one peri-urban site in Veszprém and also in Budapest, broken down for each field survey.

Table 6.1. Density and number of active bird feeders at each site, surveyed in the cities of Veszprém and Budapest, in the winter of 2021-2022.

	Site	Area of site (km ²)	Number of active feeders			Density of active feeders (/km ²)			
			Survey No.1	Survey No.2	Survey No.3	Survey No.1	Survey No.2	Survey No.3	Mean
Veszprém	A) City centre I	0.12	13	15	11	108.3	125.0	91.7	108.3
	B) Office area I	0.333	20	22	26	60.1	66.1	78.1	68.1
	C) Residential area I	0.209	27	33	28	129.2	157.9	134.0	140.4
	D) Residential area II	0.131	23	24	27	175.6	183.2	206.1	188.3
	I) Peri-urban woodland I	0.292	4	3	1	13.7	10.3	3.4	9.1
Budapest	E) Office area II	0.15	6	4	7	40.0	26.7	46.7	37.8
	F) Urban park	0.258	8	6	6	31.0	23.3	23.3	25.8
	G) Residential area III	0.299	9	12	11	30.1	40.1	36.8	35.7
	H) City centre II	0.265	14	22	18	52.8	83.0	67.9	67.9
	J) Peri-urban woodland II	0.346	4	5	5	11.6	14.5	14.5	13.5

Feeder and food types

The most frequent type of currently active feeders was type 5 (mixed feeders) and the least frequent was type 4 (food scattered on the ground) both in Veszprém and Budapest (Figure 6.3). Fat balls, seed mixes, and sunflower seeds were by far the most popular types of food that people provided to birds both in Veszprém and Budapest (Figure 6.4). However, in Veszprém those feeder types were present in a higher ratio than in Budapest, which were associated with the other four food types (animal fat; nuts; fruits; and human food waste; Figure 6.2). In Veszprém, we registered only eight feeders associated with birdbaths (seven in the Residential area II (D) and one in the City centre I (A), while birdbaths were present at only three feeders in Budapest, all of them in the City centre II site (H).

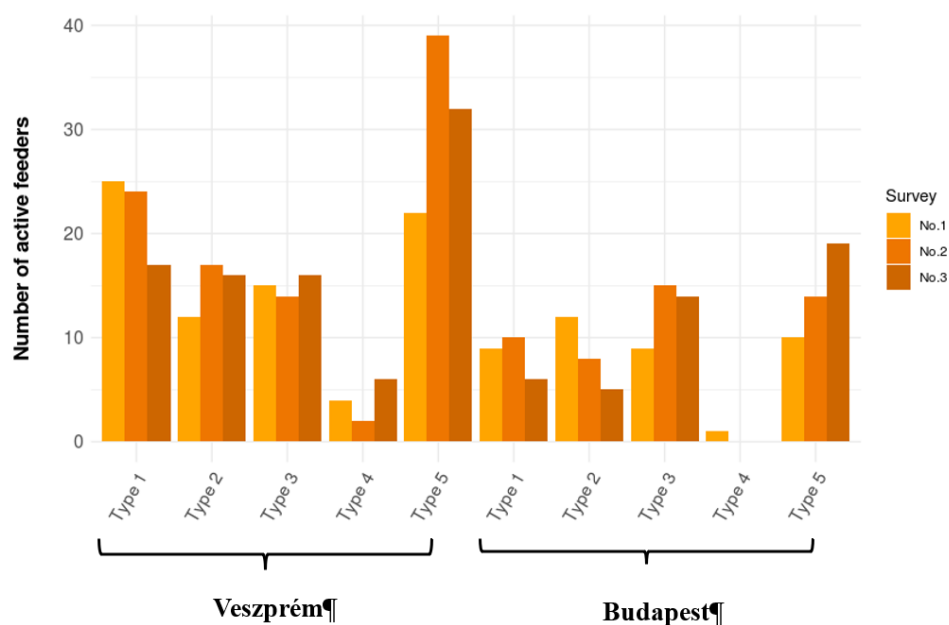


Figure 6.3. The distribution of the number and type of active bird feeders in Veszprém and Budapest. The feeder types were: (1) typical bird table often with a roof; (2) bottle-type hanging feeders providing seeds; (3) fat balls; (4) food scattered on the ground; and (5) mixed feeders where more than one feeder types were present together.

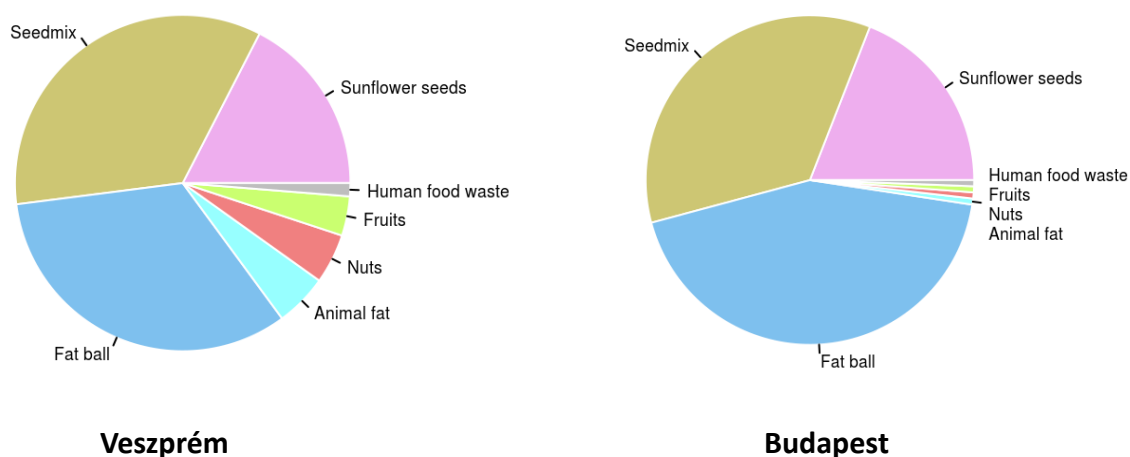


Figure 6.4. Ratio of different food types, provided by people in bird feeders in Veszprém and Budapest. We categorized the type of food provided at the feeders into seven main categories: (1) sunflower seeds; (2) seed mix; (3) fat ball (fat mixed with seeds); (4) animal fat; (5) nuts; (6) fruits; and (7) human food waste (e.g. bread, oat or cooked rice).

Number of birds

We recorded a total number of 516 individuals belonging to 24 species visiting the bird feeders (Veszprém: 20 species, Budapest: 14 species; Appendix Table S6.1). There was no significant difference in the number of birds present on the feeders per survey between the two cities (Table 6.2). However, we found significant differences in the number of birds visiting the different feeder types (Table 6.2 and 6.3): feeder type 3 (fat balls) had the lowest (compared to type 1, 2, or 5 feeders), while the highest number of individuals was observed at feeder type 5 (mixed feeders), but this difference was statistically significant only compared to feeder type 3 (Table 6.2 and 6.3). Furthermore, both daily minimum temperature (estimate $\pm$ SE = -0.087 ± 0.019) and the date (estimate $\pm$ SE = -0.006 ± 0.002) had significantly negative impact on the number of birds, while the presence of a birdbath (estimate $\pm$ SE = 1.002 ± 0.329) had a significantly positive effect on the number of birds (Table 6.3).

Table 6.2. The effect of feeder type, daily minimum temperature, date, the city (Veszprém or Budapest), and the presence of a birdbath on the number of birds observed on winter feeders.

Predictors	Chisq	df	p-value	The type 3 ANOVA (analysis of variance) results are from a generalized linear mixed-effects model using Template Model Builder, with Poisson distribution and feeder ID as a random factor. Statistically significant ($P < 0.05$) differences are highlighted in bold. N=516 individuals in 412 active feeders.
Intercept	6.217	1	0.012	
Feeder type	42.338	4	<0.001	
Daily min. temperature	19.995	1	<0.001	
Date	7.639	1	0.005	
City	0.355	1	0.551	
Birdbath	9.25	1	0.002	

Table 6.3. Pairwise comparisons of the differences in the number of birds surveyed in different feeder types during the winter of 2021-22 in Veszprém and Budapest. Feeder types are: (1) typical bird table often with a roof; (2) bottle-type hanging feeders providing seeds; (3) fat balls; (4) food scattered on the ground; and (5) mixed feeders where more than one feeder types were present together.

Contrast	Contrast $\pm$ SE	z ratio	p-value	The table shows the results of linear Tukey contrasts that were calculated from the final model presented in Table 6.2. Statistically significant ($P < 0.05$) differences are highlighted in bold. N=516 individuals in 412 active feeders.
type 2 – type 1	0.045 ± 0.317	0.143	0.998	
type 3 – type 1	-1.346 ± 0.358	-3.757	0.001	
type 4 – type 1	-0.017 ± 0.557	-0.032	1.000	
type 5 – type 1	0.573 ± 0.263	2.176	0.171	
type 3 – type 2	-1.392 ± 0.349	-3.982	<0.001	
type 4 – type 2	-0.063 ± 0.555	-0.114	0.999	
type 5 – type 2	0.528 ± 0.223	2.359	0.114	
type 4 – type 3	1.329 ± 0.588	2.259	0.143	
type 5 – type 3	1.92 ± 0.306	6.267	< 0.001	
type 5 – type 4	0.591 ± 0.513	1.152	0.759	

Number of species

The number of species per survey significantly differed between feeder types (Table 6.4, Appendix Table S6.1): there were significantly fewer species in type 3 than in type 1, 2, or 5 feeders (Table 6.5). There was no significant difference between cities in the number of feeder-visiting bird species. The presence of a birdbath (estimate = 1.378 ± 0.354) at the feeder had significantly positive effect on the number of feeder-visiting bird species while the date and the daily minimum temperatures had no significant effect on it (Table 6.4).

Table 6.4. The effect of feeder type, daily minimum temperature, date, the city (Veszprém or Budapest), and the presence of a birdbath on the number of bird species observed on winter feeders.

Predictors	Chisq	df	p-value	The table shows type 3 ANOVA (analysis of variance) results from the generalized linear mixed-effects model using Template Model Builder, with Poisson distribution and feeder ID as a random factor. Statistically significant ($P < 0.05$) differences are highlighted in bold and marginally nonsignificant ($0.05 < P < 0.1$) differences are highlighted in italics. N=516 individuals (24 species) in 412 active feeders.
Intercept	3.713	1	<i>0.053</i>	
Feeder type	22.87	4	<0.001	
Daily min. temperature	0.795	1	0.372	
Date	0.652	1	0.419	
City	2.843	1	<i>0.091</i>	
Birdbath	15.105	1	<0.001	

Table 6.5. Pairwise comparisons of the differences in the number of bird species surveyed on the different feeder types during the winter of 2021-22 in Veszprém and Budapest. Feeder types are the following: (1) typical bird table often with a roof; (2) bottle-type hanging feeders providing seeds; (3) fat balls; (4) food scattered on the ground; and (5) mixed feeders where more than one feeder types were present together.

Contrast	Contrast $\pm$ SE	z value	p-value	The table shows the results of linear Tukey contrasts that were calculated from the final model presented in Table 6.3. Statistically significant ($P < 0.05$) differences are highlighted in bold. N=516 individuals (24 species) in 412 active feeders.
type 2 – type 1	0.085 ± 0.292	0.292	0.998	
type 3 – type 1	-1.244 ± 0.372	-3.340	0.006	
type 4 – type 1	0.017 ± 0.56	0.032	1.000	
type 5 – type 1	0.374 ± 0.254	1.472	0.558	
type 3 – type 2	-1.329 ± 0.373	-3.565	0.002	
type 4 – type 2	-0.067 ± 0.565	-0.12	0.999	
type 5 – type 2	0.288 ± 0.241	1.194	0.737	
type 4 – type 3	1.261 ± 0.612	2.06	0.219	
type 5 – type 3	1.618 ± 0.339	4.766	<0.001	
type 5 – type 4	0.356 ± 0.541	0.658	0.961	

Discussion

In this study, we conducted field surveys in two Hungarian cities to assess the prevalence of residents' winter bird-feeding practices. We focused on quantifying the density and characteristics of winter bird feeders and also recorded the bird species and number of individuals visiting various feeder types.

The mixed feeder emerged as the most common feeder type in both cities, indicating a widespread attempt of the residents to offer a diverse array of bird food, likely to attract a larger number of birds to the bird tables. During the field surveys, we observed the highest number and diversity of birds in the mixed feeders, which supports the effectiveness of this practice. However, it is important to note, that this result could be attributed to the overall larger size and the higher variety of food available in mixed feeders, making them more accessible to a broader range of birds compared e.g. to fat balls, which are generally smaller and offer mostly fat and to a smaller degree, seeds. In addition, our observations revealed that feeders combined with birdbaths, irrespective of the feeder type, attracted the highest number of individuals and species. This finding underlines the importance of water sources, alongside food, for birds during the winter, emphasizing the value of birdbaths in supporting bird populations in urban environments.

The most frequent food types offered at feeders were fat balls and seed mixes, likely due to their easy commercial availability on supermarket shelves. This observation aligns with the findings by Orros and Fellowes (2015), who reported that among the UK citizens who provide food for wild birds, various seed mixes (including millet, barley, and sunflower seeds) are the most common. This food type is accepted and favoured as winter food by several bird species, especially granivores, due to its high energy content (Horn et al., 2014; Tryjanowski et al., 2018). However, several species that are relatively common in urban environments (like robins, blackbirds, or woodpeckers) do not prefer or cannot utilize seed mixes as food source, therefore making these feeders less suitable for supporting a diverse winter bird community (Galbraith et al., 2015; Horn & Johansen, 2013; Støstad et al., 2017).

Our study revealed a notably higher density of feeders in the urban sites of Veszprém (a medium-sized town) compared to Budapest (a metropolis, and the capital city of Hungary). We also found that feeder densities were notably the highest in the residential areas of Veszprém (range: 129.2–206.1 bird feeders/ km²). This variation highlights the influence of the urban landscape structure on birds' winter food availability (Ciach & Fröhlich, 2017). In Veszprém, these study sites were situated in block housing areas and detached houses with private gardens with interconnected green spaces, whereas, in Budapest, the study sites were in densely built-up areas with green spaces resembling more like small, "isolated islands"

within the urban landscape. In addition to the cities' architectural structure, other factors could also play a role in shaping bird feeder densities, such as differences in the attitude of the residents between the cities or city districts, or local regulations that sometimes prohibit bird feeding near apartments due to the attraction of unwanted guests on bird feeders, like city-dwelling pigeons or rodents. These type of regulations are present in both Veszprém and Budapest. However, Budapest is a bigger and more densely populated city, also with more pigeons (Appendix Table S6.1), thus these types of regulations are probably more frequent and prevalent there, which could also negatively affect the number of bird feeders there. Our results revealed a remarkable and fine-scale (i.e., within-city) variation in the availability of winter bird feeders – and consequently food supply – that probably influence various aspects of birds' biology, including physical condition, physiological stress, behaviour (Broggi et al., 2005; Lawson et al., 2018; Roth & Vetter, 2008), and most importantly, birds' chances of survival during the winter months. Therefore, we suggest that future studies focusing on the survival patterns of urban birds should consider this factor rather than treating distinct parts of the city with different landscape structures as the same.

In contrast to the urban sites, our data showed seemingly no difference in the density of feeders between the two peri-urban woodlands, where feeder density was markedly lower than in the city (Figure 6.2.), similarly to the findings of Tryjanowski, Skórka et al. (2015). Even though, the vegetation of these two sites is quite different from each other (also from the urban sites too), both are characterized by the low rate of built-in areas (mostly weekend houses) and low human population density, which could explain the similarly low bird feeder densities at both sites.

Finally, it is important to acknowledge the limitations of our study. Our chances of detecting bird feeders might have varied between or even within cities, due to the different architectural layout of buildings, green spaces, and private properties. During the surveys, we were looking for bird feeders visually, making it challenging to spot feeders located high above the ground (e.g. on a fourth-floor balcony or windowsill) or completely hidden within private gardens. This difficulty may have had a greater impact on our results regarding food type and the presence of birdbaths, as a good view of the feeding station is important to reliably collect such data. Moreover, the differences we found in the distribution of birdbaths across cities and study sites might partially result from the initial inconsistency among surveyors in recording the presence of birdbaths. Nonetheless, we believe that our feeder density results were less affected by these difficulties, as the presence of an active feeder could be often inferred from birds' activity and vocal cues even if we did not have a clear view of the feeder's exact location.

7. General discussion

In my thesis, I explored the effects of urbanisation on great tits' behaviour and population demography parameters. In this final chapter, I discuss the main findings (*Chapter 3-6.*) and also make some suggestions on how future urban research and planning could support local wildlife, which is essential for creating more sustainable cities.

During the last decades, several studies showed that urban birds (including great tits) often have lower reproductive success per nesting attempt than their forest conspecifics (Chamberlain et al., 2009; Rodewald & Gehrt, 2014; Seress & Liker, 2015). However, this may not necessarily result in lower annual reproductive success in cities, if urban parent birds respond with an increased propensity of seasonally second broods to increase their overall reproductive outcome (Cornell & Williams, 2016; Hoffmann et al., 2015). However, this possibility was often overlooked by previous research – even in those studies that worked on populations in which seasonally second broods are not uncommon (Arriero et al., 2006; de Satgé et al., 2019; Gładalski et al., 2016; Van De Castele et al., 2003), sometimes outright stating that second broods are omitted from analysis, even though second broods exceed ~20% of first broods within a breeding season (Sasvári & Orell, 1992). Therefore, at first, we compared the probability of double-brooding and the total number of annually fledged chicks per female between urban and forest habitats (*Chapter 3.*). Although we found a trend towards a higher probability of double-brooding in the urban habitat type compared to the forest habitat type, this difference was not statistically significant and was not consistent across the two forest sites. Double-brooding increased the reproductive success of female great tits in both habitat types, but our results also clearly indicate that urban females cannot effectively compensate in this way for their significantly lower reproductive output per brood. Thus, the annual reproductive success of great tits was clearly lower in urban than in forest habitats. However, as I discussed in the chapter 2. (*General field methods*), other mechanisms, like increased survival, can still effectively mitigate the habitat differences in birds' lifetime reproductive success.

So as a next step, we compared annual variation in apparent survival probabilities of adult great tits at our two forest and two urban study sites (*Chapter 4.*). Contrary to my initial hypothesis, urbanisation did not consistently increase birds' survival probabilities: the sites both with the lowest and highest estimates of survival were urban habitats. Survival probabilities decreased with birds' age at both urban sites in most years, but such patterns were not detected at forest sites. The results demonstrate that the demographic factors regulating populations can vary not only between but also within habitat types and highlight

the importance of studies with multiple study sites, in order to get an accurate picture of how urbanisation affects survival and other parameters of populations' demography.

A strongly decreased annual reproductive success in any population, without increased adult survival, questions the self-sustaining capability of the given population (Bartos Smith et al., 2016). Thus, in the case of urban populations, there is a reasonable possibility that permanent immigration from surrounding natural habitats is needed for sustainability. Estimating the permanent migration of individuals between populations is an especially challenging task and therefore these types of data are quite rare in ecological studies (Murray & Sandercock, 2020). In a recent study, our research group tested the genetic differentiation between two of the breeding populations of great tits also included in my thesis (Veszprém and ~4 km from there Vilma-pusztá, one of the forest sites; see *Chapter 2. General field methods*). This study found low genetic differentiation and a detectable gene flow between the two sites, and the results did not suggest asymmetry in the direction of migration (Mihalik et al., 2024 under submission). So, these two populations are probably genetically connected, and the evidence does not support a source-sink population relationship between them. In contrast, in Barcelona, Spain, researchers found that the gene flow from the urban great tits' population to the forest was higher than the other way (Björklund et al., 2010), which also does not support the urban sink population hypothesis. In my opinion, genetic studies like these could help to understand the connection between urban and rural animal populations, but cannot substitute the actual tracking data of individuals' movements combined with life-history traits (for example: adult dispersal and natal dispersal with reproductive success) and we need future studies to provide these types of information. Ideally, long-term telemetry tracking would provide information not just about the birds' survival but also about dispersal throughout different life stages, such as post-fledging, overwintering adults, breeding adults, and more. This method would provide a much more detailed dataset thus, allowing scientists to calculate survival probabilities for different life stages and thus identify which stage is the most vulnerable for a given species or population. In addition, the dispersal rate of birds usually differs between life stages and sexes (Garant et al., 2005; Kingma et al., 2017), which biases the survival estimates using traditional mark-recapture methods (Murray & Sandercock, 2020). However, tracking the movements of individuals may eliminate this bias, and also allows researchers to determine the dispersal rate at each life stage. On the other hand, further research is also needed to investigate the possible shift of other demographic factors in urban bird populations, like post-fledging survival, and natal dispersal (Sepp et al., 2018). Now, there is a major knowledge gap about how these factors are shaping the urban populations' growth rates and dynamics. Future research is needed to investigate these other

demographic factors in order to get a proper understanding of whether or not our cities are viable habitats for birds without the resupply from natural habitats.

Several studies have investigated the variations in life-history traits between rural and urban populations of passerines. The idea of a pace-of-life syndrome characterizes the differences in inter- and intraspecific life-history traits along a continuum that ranges from slow to fast paces of life, with long lifespans, low reproductive and metabolic rates, and heightened somatic defences at the slow end, and the opposite traits at the fast end (Sepp et al., 2018). The smaller clutch sizes of urban birds may mean that in the less favourable environment, parents simply invest less energy in reproduction per breeding season, thus increasing their lifespan and so lifetime reproductive success. However, it does not seem likely that passerines in urbanised breeding habitats reduce their energy investment in annual reproduction (Demeyrier et al., 2016). Furthermore, several previous studies show that urban parents invest not less but, on the contrary, more energy in raising chicks compared to their counterparts in natural habitats. For example, urban great tit parents tend to fly further from their nest in order to find prey (Jarrett et al., 2020) and increase the chick-feeding frequency to provide a sufficient amount of food for their nestlings (Isaksson & Andersson, 2007; Pollock et al., 2017; Sinkovics, 2014). In addition, since they possibly only have 1-2 breeding seasons before they die, the common life-history strategy for short-lived species is to invest as much as possible each year, since their chance of seeing the next spring is typically fifty-fifty (Dobson, 1987; Jansen et al., 2014; Thaxter et al., 2006). According to this hypothesis, the survival probability of short-lived species does not decrease significantly as a result of increased reproductive costs. Results from several nest manipulation studies point in this direction. Over nine years, in Wytham Wood, Oxford, Pettifor and his colleagues removed 3-4 chicks from some great tits' nests immediately after hatching, added 3-4 chicks to others, and left some nests unmanipulated (Pettifor et al., 2001). Neither type of nest size manipulation affected the survival probability of the female or the male parents. The researchers found similar results when they added 1-2 chicks to blue tits' nests: although parents' feeding frequency increased, their survival probability did not decrease (Parejo & Danchin, 2006).

In line with this, we also found (*Chapter 3.*) that the annual reproductive success of birds was lower in cities. However, the fact that we did not find a consistently higher survival in urban sites (described in *Chapter 4.*) questions the assumption that it is indeed the case that urban great tits have slower pace-of-life, at least in our study populations. However, the assumption that urban environments favour slower life-history strategies is not always accurate, and the reality is much more complex. As a recent review article analysed life-history traits of 17 mammal and avian species (including great tits), their results pointed out

that individual life histories within a population are highly divergent and not structured by a slow–fast continuum (Van De Walle et al., 2023). Cities represent a relatively new habitat type so the adaptation process to the new environment is in an early stage for several species (Liker, 2020; Møller et al., 2012). Along with that, urban populations could have increased diversity in several individual traits, compared to natural areas. As two review studies from the last three years showed, urban bird populations have higher phenotypic variation compared to their rural counterparts, and the increased phenotypic variance can result from underlying genetic variation or plasticity, conceivably due to higher landscape heterogeneity in cities (Capilla-Lasheras et al., 2022; Thompson et al., 2021).

Generally, as the first step in adaptation, the behaviour of individuals shifts (Egbert & Pérez-Mercader, 2016; Jean Piaget, 2006; Shelton & Martins, 2016). For example, successfully urbanised bird species are found to be singing earlier in spring (Møller et al., 2015) or tolerate people better (Symonds et al., 2016). Behavioural response is essential for individuals to be able to successfully utilize (new) resources in an ever-changing environment (Preisner et al., 2017). Thus, the challenge of food limitation probably leads to behavioural responses of urban birds too. To investigate how parent birds utilize food sources in cities, we employed radio-telemetry tracking and real-time observations on urban-breeding great tits' habitat use, combined with detailed plant surveys and video recordings of nestlings' diet (*Chapter 5*). We found that the availability of bird feeders strongly affected birds' habitat use and that besides tree canopies, birds also frequently foraged on the ground. Since bird feeders are typically missing from forest habitats (Tryjanowski et al., 2015), as was also shown in *Chapter 6*, the use of this type of novel nestling food source itself can induce altered behaviour of urban parents. Also, foraging great tits generally avoided non-native plants, particularly broadleaved species, and were more likely to forage on and deliver nestling food from large native trees. The reason for this is presumably that lower amounts of prey insects could be found on non-native plants than on large, native trees (Burghardt et al., 2010) and parent birds altered their behaviour to be able to collect prey more efficiently (Jarrett et al., 2020). These behavioural shifts are probably a sign of adaptation to the urbanised breeding habitat, but additional research is needed, where researchers compare the habitat use of other species and taxa in urban and natural areas.

The types and amount of food sources for birds considerably differ between urban and non-urban habitats not just during the breeding season, but also in the winter time (Tryjanowski et al., 2015). Cities offer a more favourable habitat for many wintering birds compared to natural areas, primarily due to the increased availability of the winter food sources provided by people. Bird feeding is one of the most popular human-wildlife

interactions globally (Jones & Reynolds, 2008). So, to investigate this aspect of urbanisation too, we surveyed bird feeders during the winter of 2021-22 in two cities in Veszprém and Budapest (*Chapter 6*). The most frequent food types were fat balls, seed mix, and sunflower seeds in both cities. However, the density of feeders was higher in Veszprém, a middle-sized city compared to Budapest. The lower feeder density can also mean less food for the birds, which can lead to decreased body condition during the winter (Goławski et al., 2015; Plummer et al., 2018) or a decreased probability of surviving the winter in Budapest compared to Veszprém. Unfortunately, we do not have such a long-term dataset for survival analysis for available for Budapest as for Veszprém, although it will be an instructive future study, where we will be able to compare the survival of adult birds between cities where different amounts of human-provided winter food are available. After all, as the results of our study above show that while the survival probability of adult birds may differ between cities, this difference is not necessarily apparent among the populations of surrounding natural areas. Cities represent a highly heterogeneous habitat type and several factors could vary between city and city affecting passerine birds' survival. Less traffic and a lower proportion of large glass surfaces in buildings could reduce collision rates (Loss et al., 2015), local predator populations of native and non-native species could be different (Murgui & Hedblom, 2017), and the local microclimate could also affect bird survival (Robinson et al., 2007; Salewski et al., 2013). One of the main reasons for the altered survival of urban birds, could be that human activities have a strong influence on the amount of winter food in urban habitats, and this can cause significant between-cities differences in the winter survival. Meanwhile, in forest sites, humans usually do not provide additional food supplies for passerines. But in many forests, also in our two forest study sites, hunters actively feed big games (e.g. deer and wild boar) with grains, and birds certainly could exploit these food sources.

Further research is required to collect data on the types of food sources used by avian species during the wintering period in different habitats. Additionally, it would be beneficial to compare the impact of human habitat use, such as urbanisation or agriculture, on the food supplies of local wintering birds. Theories suggest that in the temperate zone, wintering passerines may move from the surrounding natural habitats to urban areas during the winter, in part due to the milder microclimate and the increased availability of food (Chace & Walsh, 2006; Seress & Liker, 2015). Nevertheless, further research is needed to confirm this hypothesis, as former studies have primarily focused on the composition of wintering bird communities rather than tracking individual movements or habitat use (but see: St. Clair et al., 1998). Despite this, if the theory is valid and some passerines are indeed moving to cities for the winter, it could be a primary factor in the absence of genetic isolation between urban and

forest bird populations, and could also indicate that forests serve as a source habitats for populations in urban areas (Møller et al., 2014; Waits et al., 2008).

On the other hand, population viability analysis (PVA) provides an excellent way of understanding whether urban bird populations are self-sustaining or not (Possingham et al., 2013). PVA models consider vital rates, life-history traits, and habitat associations to predict the viability or persistence of a population or a species under current or simulated future conditions and guide conservation and management efforts (Crawford et al., 2018; Wenger et al., 2017). Former PVA studies have already been carried out on some urban bird species, such as golden-cheeked warbler (*Setophaga chrysoparia*) or Carolina chickadees (*Poecile carolinensis*), but unfortunately, the results showed that urban populations of these species declined toward local extinction (Narango et al., 2018; Reidy et al., 2020; but see Smith et al., 2016). This result led researchers to suggest that in some cases, the seemingly stable urban bird populations could be maintained by the immigration of individuals from surrounding natural areas (Reidy et al., 2020). Still, only very few research have modelled the viability of urban bird populations, especially outside of the temperate zone, thus future studies will importantly add to our knowledge of urban bird populations' viability by continuing to assess demography patterns, as well as identifying the factors that mold them (Leveau & Zuria, 2017).

Results of my doctoral studies show, that urbanisation does not have a clear, black-and-white effect on bird populations. We, the researchers try to explore and understand the impact of urbanisation on wildlife, while we still do not fully understand the environmental and ecological effects that drive species' demographic patterns in their natural environment. In my opinion, while the recent results of my doctoral studies have great significance as the urbanised areas expand all around the globe, the scientific community should investigate further aspects of populations' demography in different types of other human-transformed habitat types, like agricultural landscapes, which cover 36.8% of global land surface by 2021 (in Hungary this number was much higher, 55.3% according to the World Data Bank: <https://data.worldbank.org/indicator/AG.LND.AGRI.ZS>).

Urbanisation is a complex process with divergent effects on the local biotic and abiotic environment of which we humans are also an active part. There are large differences both within and between cities in geography, climate, age, human population density, and socio-economic status (United Nations Human Settlements Programme, 2022). What seems to be common in every city on the planet is that residents still looking for the connection with nature and wildlife (Cox & Gaston, 2015; Dayer et al., 2019; Soga & Gaston, 2020). If they can do so, their mental and physiological health could benefit from it (Soga et al., 2021;

Vujcic et al., 2017). Creating greener cities in the present and the future with the active involvement of the residents would help to create healthy local communities and preserve local biodiversity. In this process, the work of scientists is essential to collect and share the knowledge about the ecology of urban habitats.

Fortunately, several simple steps can be taken by citizens to improve habitat quality for local wildlife in cities. An important step would be if residents kept their cats indoors and refrained from allowing them to roam and hunt outside, ultimately resulting in the deaths of hundreds of birds, reptiles, and small mammals (per cat) as I discussed in the *1.1 General Introduction* (Baker et al., 2005; Loss & Marra, 2017). As I also mentioned before, collisions with buildings and vehicles could be a lead mortality cause in urban animal populations, thus another important step would be to minimize the use of cars as much as possible and maintain adherence to speed limits when driving. Not surprisingly, an increase in traffic leads to a rise in the number of animals struck by vehicles, as demonstrated by studies conducted in Turkey (Balčiauskas et al., 2023; Özcan et al., 2022). Furthermore, the growing number of cars in cities has resulted in an increase in parking spaces, which, in many instances, also results in the paving over of green spaces, such as parks and tree lanes along streets. Lastly, I would personally recommend getting informed about local environmental and wildlife protection policies and reporting any violations of these policies to the relevant authorities (for example in Hungary the illegal dumping of household/electric/construction waste or the destruction of swallow nests in residential and business buildings). In my opinion, people must realise that they can make a difference themselves, not wait for someone else to do it for them.

Let me close my lines with Albert Szent-Györgyi's words: "*Nem lehet általában azt mondani, hogy jó és rossz környezet, mert ha egy halat kiveszek a vízből és kiteszem a legszebb fűre, az annak nem jó környezet. De ha egy nyulat beteszek a tengerbe, az neki nem lesz jó környezet. Szóval nincs jó és rossz környezet, csak az a jó, amihez hozzá vagyunk "szabva".*"

8. Thesis points

1. Using great tits as a model system, I showed, that a higher ratio of second broods within one breeding season can not compensate for birds' lower breeding success in urban habitats. I found that urban birds tend to have a slightly higher probability of double-brooding (44% of females) compared to forest birds (36%), but this difference was not statistically significant and consistent between the two urban study sites. At the same time, double-brooded urban females produced a similar number of fledglings per season as single-brooded forest females. My results showed that both single- and double-brooded females produced significantly fewer fledglings annually in the cities than in the forests.
2. I used mark-recapture modelling to estimate the apparent survival probabilities of adult great tits in two urban and two forest breeding populations. My results showed that urbanisation did not have a consistent effect on survival, because both the lowest and highest survival estimates were obtained for urban sites and estimates for the two forest sites were in between. I found that the study year affected the birds' survival and males usually have slightly higher survival during the study period in all four sites. The age of the birds did not have a strong effect in the forest, only in the urban sites, and the nest box occupancy rate (an estimate for breeding density) did not appear to affect annual survival.
3. We successfully employed radio-telemetry tracking to characterize urban-breeding great tits' habitat use. Moreover, we combined the radio tracking with real-time field observations, video recordings of nestlings' diet, and detailed plant surveys. Parent birds were more likely to forage on and deliver nestling food from large native trees, foraged less on and collected fewer prey items from the most abundant tree species, and generally avoided non-native plants, particularly broadleaved species. Interestingly, we found that birds frequently foraged on the ground. We also found that the availability of bird feeders strongly affected birds' habitat use.
4. We successfully surveyed the active winter bird feeders in two cities, and nearby peri-urban woodlands. I found that the density of feeders was higher in Veszprém than in Budapest, but I did not find this difference between the two peri-urban woodlands. In both cities, the most frequent food types were fat balls, seed mix, and sunflower seeds. I found that the type of the feeder, but not the city, significantly affected both the number of individuals and species visiting bird feeders.

9. Tézispontok

1. Kimutattam, hogy a másodköltések nagyobb arányával a madarak nem képesek kompenzálni az alacsonyabb költési sikert a városi élőhelyeken. Eredményeim alapján továbbá elmondható, hogy a városi széncinege tojók nagyobb valószínűséggel kezdenek másodköltésbe (a tojók 44%-a), mint erdei fajtársaik (36%), de ez a különbség nem volt konzisztens a két vizsgált városi helyszín között. Az évente kireptetett fiókák száma alacsonyabb volt a két városi populációban, mint a két erdeiben, mind az egyszer, mind a kétszer fészkelő tojók esetében. Ez a különbség annyira jelentős, hogy a városi élőhelyen csak a másodköltő tojók tudtak annyi fiókát kireptetni egy évben, mint az erdei élőhelyen az egyszer költő tojók.

2. Jelölés-visszafogás adatok felhasználásával sikeresen megbecsültem az adult széncinegék látszólagos, éves túlélési valószínűségét a két városi és két erdei költőpopulációkban. Eredményeim azt mutatták, hogy az urbanizáció hatása nem volt konzisztens, mivel a négy vizsgálati helyszín közül a legmagasabb és a legalacsonyabb túlélési valószínűséget is városi élőhelyen regisztráltuk, míg a két erdei helyszín e kettő közötti értékeket vett fel minden évben. A madarak túlélésére a vizsgálati évnél volt hatása és a hímeknek általában valamivel jobb volt a túlélése a tojókhoz képest a vizsgálati időszak alatt mind a négy helyszínen. A madarak életkora nem volt erős hatással az erdei élőhelyeken, csak a városi területeken, továbbá az odúk foglaltsági aránya (a költési sűrűség iránymutatója) nem befolyásolta a túlélést.

3. Sikeresen alkalmaztunk rádiótelemetriás nyomkövetést és valós idejű megfigyeléseket a városban költő cinegék territórium használatáról, miközben videofelvételeket készítettünk a szülők által hordott fiókatáplálékról és ezeket az adatokat később kombináltuk a territóriumok részletesen felmért növényzeti térképeivel. A szülő madarak nagyobb valószínűséggel táplálkoztak és hordtak fióka táplálékot a nagy méretű őshonos fákról, kevesebbet táplálkoztak és kevesebb zsákmányt gyűjtöttek a leggyakoribb fajokról, és általában kerültek a nem őshonos fajokat, különösen a lombhullatókat. Érdekes módon azt is megfigyeltük, hogy a madarak gyakran a talajon táplálkoztak. Továbbá az etetők elérhetősége is erősen befolyásolta a madarak élőhelyhasználatát.

4. Sikeresen mértük fel a téli madáretetőket 10 helyszínen két városban és azokhoz közeli erdős területeken. Az aktív etetők sűrűsége a veszprémi területeken általában magasabbnak bizonyult, mint a budapesti helyszíneken, de a város közeli erdős területek közt nem volt különbség. Az etetőkön leggyakrabban megfigyelt tápláléktípus mindkét városban a

cinkegolyó, a magkeverék és a napraforgómag volt. Az etető típusa szignifikáns hatást gyakorolt az azt látogató madarak egyed-, és fajszámaára, míg a két város között ezekben nem találtunk különbséget.

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11. List of publications

Publications and manuscripts included in the thesis

1. **Boglárka Bukor**; Gábor Seress; Ivett Pipoly; Krisztina Sándor; Csenge Sinkovics; Ernő Vincze; András Liker (2021) *Double-brooding and annual breeding success of great tits in urban and forest habitats*. Current Zoology, 2021 1-9. doi: <https://doi.org/10.1093/cz/zoab096>
2. **Boglárka Bukor**, Brett K. Sandercock; Karl L. Evans, Ivett Pipoly; Krisztina Sándor; András Liker; Gábor Seress (2025) *Site-specific impacts of urbanization on annual survival of a forest bird*. Ecology and Evolution, 2025; 15:e71140. doi: <https://doi.org/10.1002/ece3.71140>
3. **Gábor Seress**, Krisztina Sándor; Veronika Bókonyi; Boglárka Bukor; Katalin Hubai; András Liker (2025) *Radio-tracking urban breeding birds: the importance of native vegetation*. Ecological Application, 2025;35:e3095. doi: <https://doi.org/10.1002/eap.3095>
4. **Boglárka Bukor**; Boróka Kósa; András Liker; Gábor Seress (2024) *Winter field survey of bird feeders in two Hungarian cities*. Ornis Hungarica, (1): 80–95. doi: <https://doi.org/10.2478/orhu-2024-0006>

Personal contribution to the studies included in the thesis

	Study 1 (Chapter 3.)	Study 2 (Chapter 4.)	Study 3 (Chapter 5.)	Study 4 (Chapter 6.)
Original idea and design	✓	✓	X	✓
Fieldwork and data collection	✓	✓	✓	✓
Data analysis	✓	✓	X	✓
Manuscript preparation	✓	✓	X	✓

Publications and manuscripts not included in the thesis

Gábor Seress, Krisztina Sándor, Ernő Vincze, Ivett Pipoly, Boglárka Bukor, Nóra Ágh, András Liker (2021) *Contrasting effects of the COVID-19 lockdown on urban birds' reproductive success in two cities*. Scientific reports; (2021) 11:17649. doi: <https://doi.org/10.1038/s41598-021-96858-8>

Andor Pitó, Boglárka Bukor, Előd Györig, Vojtěch Brlík, Jenő Kontschán, Gergő Keve, Nóra Takács & Sándor Hornok (2024) *Investigations of the tick burden on passeriform, water-associated and predatory birds reveal new tick–host associations and habitat-related factors of tick infestation*. Parasites & Vectors, 17:144. doi: <https://doi.org/10.1186/s13071-024-06229-1>

Conference presentations and poster

Boglárka Bukor; *The frequency of re-nesting in forest and urban populations of Great Tit* (presentation); **Tudományos Diákköri Konferencia**, Budapest, 2016. 11. 23. TolnAgro special prize

Boglárka Bukor, Veronika Bókony, Tamás Hammer, Sándor Papp, Ivett Pipoly, Bálint Preiszner, Gábor Seress, Csenge Sinkovics, Ernő Vincze, András Liker; *The frequency of re-nesting in forest and urban populations of Great Tit* (poster); **XVIII. Magyar Etológus Konferencia**, Debrecen, 2016. 12. 2-4.

Boglárka Bukor, Veronika Bókony, Tamás Hammer, Sándor Papp, Ivett Pipoly, Bálint Preiszner, Gábor Seress, Csenge Sinkovics, Ernő Vincze, András Liker; *The frequency of re-nesting in forest and urban populations of Great Tit* (presentation); **Magyar Biológiai Társaság Állattani Szakosztályának 1038. előadó ülése**, Budapest, 2017. 03. 1.

Boglárka Bukor; *The frequency of re-nesting in forest and urban populations of Great Tit*; **XXXIII OTDK Biológia Szekció**, Debrecen, 2017. 04. 12. **Animal ecology, zoology I section special prize**

Boglárka Bukor, Veronika Bókony, Tamás Hammer, Sándor Papp, Ivett Pipoly, Bálint Preiszner, Gábor Seress, Csenge Sinkovics, Ernő Vincze, András Liker; *The frequency of re-nesting in forest and urban populations of Great Tit* (presentation); **19. Kolozsvári Biológus Napok**, Kolozsvár, 2018. 04. 13-14.

Boglárka Bukor, Nóra Czikkelyné Ágh, Ivett Pipoly, Krisztina Sándor, Gábor Seress, Csenge Sinkovics, Ernő Vincze, András Liker; *Annual survival of adult Great Tits in different types of breeding habitat* (presentation); **Urbanizációs Ökológiai Konferencia**, Veszprém 2018. 10. 19-20.

Boglárka Bukor; *Annual survival of adult Great Tits in different types of breeding habitat* (presentation); **Tudományos Diákköri Konferencia**, Budapest, 2018. 11. 21. **Biological Institute special prize**

Boglárka Bukor; Nóra Czikkelyné Ágh, Ivett Pipoly, Krisztina Sándor, Gábor Seress, Csenge Sinkovics, Ernő Vincze, András Liker; *Annual survival of adult Great Tits in different types of breeding habitat* (presentation); **XX. Magyar Etológus Találkozó**, Kolozsvár, 2018. 11. 23-25.

Boglárka Bukor; *Annual survival of adult Great Tits in different types of breeding habitat*; **XXXIV OTDK Biológia Szekció**, Budapest, 2019. 04. 15-17. **Animal ecology II section special prize**

Boglárka Bukor; Nóra Czikkelyné Ágh, Ivett Pipoly, Krisztina Sándor, Gábor Seress, Csenge Sinkovics, Ernő Vincze, András Liker; *Annual survival of adult Great Tits in different types of breeding habitat (presentation)*; **Student Conference on Conservation Science**, Tihany, 2019. 08. 27-31.

Boglárka Bukor; Nóra Czikkelyné Ágh, Ivett Pipoly, Krisztina Sándor, Gábor Seress, Csenge Sinkovics, Ernő Vincze, András Liker; *Annual survival of adult Great Tits in different types of breeding habitat (presentation)*; **Darwin Days**, Tihany, 2020. 02. 11-13.

Boglárka Bukor; *The influence of habitat and female traits on the probability of double-brooding and annual breeding success in great tits (presentation)*; **Pannon Tudományos Nap**; online; 2020. 11. 16-17.

Ernő Vincze, Nóra Ágh, Gábor Seress, Ivett Pipoly, Krisztina Sándor, Boglárka Bukor, Zsolt Rónai, Krisztina Molnár, András Liker; *Is there a relationship between DRD4 genotypes and risk-taking behaviour of female great tits in urban and forest habitats? (presentation)*; **XXII. Magyar Etológus Találkozó**, online, 2020. 12. 04-05.

Boglárka Bukor; Gábor Seress, Ivett Pipoly, Krisztina Sándor, Csenge Sinkovics, Ernő Vincze, András Liker; *The influence of habitat and female traits on the probability of double-brooding and annual breeding success in great tits (presentation)*; **XXII. Magyar Etológus Találkozó**, online, 2020. 12. 04-05.

Boglárka Bukor; Gábor Seress, Ivett Pipoly, Krisztina Sándor, Csenge Sinkovics, Ernő Vincze, András Liker; *Double brooding and annual breeding success of great tits (*Parus major*) in urban and forest habitats (presentation)*; **Behaviour, Ecology and Evolution (BEE)**, online, 2021. 03. 07-08.

Boglárka Bukor; Gábor Seress, Ivett Pipoly, Krisztina Sándor, Csenge Sinkovics, Ernő Vincze, András Liker; *Double brooding and annual breeding success of great tits (*Parus major*) in urban and forest habitats (presentation)*; **12. Magyar Ökológus Kongresszus**, Vác, 2021. 08. 24-26.

Boglárka Bukor, Brett Sandercock, Ivett Pipoly, Krisztina Sándor, Gábor Seress^o, András Liker^o; *Survival probability of great tits in forest and city: different influencing factors between habitats (presentation)*; **Magyar Etológiai Társaság XXIV. Konferenciája**, Budapest, 2022. November 25-27.

Boglárka Bukor, Boróka Kósa, Liker András, Seress Gábor; *Téli madáretetőik terepi felmérése, Budapesten és Veszprémben (presentation)*; **Kolozsvári Biológus Napok**, Kolozsvár, 2023. 03.31-04.01.

Bukor Boglárka, Nolwenn Fresneau, Liker András; *Szociális poligámia megfigyelése egy monogám énekesmadár fajnál (presentation)*; **XXV Magyar Etológus Találkozó**; Debrecen; 2023. 10. 26-28

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