DOCTORAL (PHD) DISSERTATION

THE EFFECTS OF URBAN ENVIRONMENT ON REPRODUCTIVE SUCCESS AND PLUMAGE CHARACTERISTICS OF BIRDS

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THE EFFECTS OF URBAN ENVIRONMENT ON REPRODUCTIVE SUCCESS AND PLUMAGE CHARACTERISTICS OF BIRDS

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ABSTRACT IN ENGLISH

Urbanization is one of the strongest habitat transforming processes that poses several challenges to wildlife. The urban environment differs from the natural areas in many aspects, such as the changed amount and quality of natural food sources and warmer microclimate that can have significant impacts on the success of urban birds.

In my PhD research, I examined the effects of these altered environmental factors on reproductive success and plumage characteristics of great tits *(Parus major)*. Using experimental manipulation of nestling food in wild great tits, I showed that the poorer reproductive success and smaller body size of nestlings in the studied urban site are mainly caused by food limitation: food supplementation almost completely eliminated differences between urban and forest broods in these components of breeding success.

I also performed two correlative studies, in which I investigated the effects of the urban environment on the number and structural properties of feathers. Comparing the structural properties of feathers between urban and forest great tits, I found differences in only a few feather traits, and these were present only in first year birds. Specifically, I showed that the contour feathers of first year birds had a looser structure in urban than in forest populations, which may promote better heat dissipation – suggesting adaptation to the warmer urban microclimate. Furthermore, I found differences in two traits of first year birds' wing feathers: urban birds had narrower rachises and higher barbule densities, which may indicate nutritional constraints during the feather growth period. However, I did not find any differences in the feather structure of adult birds between urban and forest populations. This latter finding can be explained by reduced sensitivity of adults to environmental effects, or by selective mortality within first year birds that eliminates first year birds with poorer structural properties of their wing feathers.

To examine plumage characteristics related to feather number, I developed a novel non-invasive method. I showed that urban nestlings had fewer contour feathers and smaller feather tract area, which suggests larger bare body surfaces than in nestlings reared in forest habitats. These changes in the plumage of urban birds may promote better heat dissipation, suggesting adaptation to the urban warmer microclimate. To better understand the exact environmental causes and fitness effects of these plumage changes in urban bird populations, further experimental studies would be needed. My results contribute to the understanding of the effects of one of the globally most significant environmental impacts on birds and point out that there are still very under-researched areas on this topic that could serve as a basis for several future studies.

MAGYAR KIVONAT

Az urbanizáció napjainkban az egyik legerőteljesebb élőhely átalakító folyamat, ami komoly kihívás elé állítja az élővilágot. A városi környezetben például a rovarevő madarak kevesebb jó minőségű táplálékhoz jutnak, valamint magasabb a környezetük átlagos hőmérséklete is, ami jelentős hatást gyakorolhat a városi egyedeik sikerességére.

Doktori tanulmányaim során e megváltozott környezeti tényezők hatásait vizsgáltam a széncinegék *(Parus major)* szaporodási sikerére és tollazati jellemzőire. Egy táplálék-manipulációs terepi vizsgálat keretében kimutattam, hogy a vizsgált városi helyszínen a széncinegék gyengébb szaporodási sikerének és a fiókák kisebb testméretének fő oka a táplálléklimitáció. A táplálékkiegészítés közel teljesen eltűntette a városi és az erdei fészekaljak között megfigyelt különbségeket a szaporodási siker vizsgált változói esetében.

Két további korrelatív vizsgálatban a városi környezet madarak tollazati jellemzőire gyakorolt hatásait kutattam. A tollak szerkezeti tulajdonságait vizsgálva csak néhány eltérést találtam az élőhelyek között, és a tapasztalt különbségek kizárólag az elsőéves madarak között voltak megfigyelhetők. Kimutattam, hogy a városi elsőéves madarak testtollai lazább szerkezetűek az erdeiekéhez képest, ez pedig a jobb hőleadást segítheti elő, ami a melegebb környezethez történő adaptációra utalhat. Emellett az elsőéves madarak szárnytollain is megfigyeltem néhány élőhelyi eltérést (keskenyebb tollszár, magasabb ágacskasűrűség), amelyek viszont a táplálékhiány hatásait jelezhetik. A felnőtt madarak esetében viszont nem találtam különbséget a városi és az erdei populációk tollszerkezetében, ami arra utalhat, hogy a felnőtt madarak kevésbé érzékenyek ezekre a környezeti hatásokra. Az eltérés hiánya azonban az elsőéves madarak szelektív mortalitására is utalhat, amelyben szerepet játszhat a repülőtollak gyengébb minősége is.

Mindemellett kifejlesztettem egy új, noninvazív módszert a tollazat sűrűségének vizsgálatára, amellyel kimutattam, hogy a városi széncinege fiókák kevesebb testtollal és kisebb területű tollsávokkal rendelkeznek, ami az erdei madarakhoz képest relatíve nagyobb csupasz testfelületekre utal. E változások a városi környezetben a jobb hőleadást szolgálhatják, ami a szintén a városi mikroklímához történő adaptáció folyamataira utalhat. Ahhoz, hogy jobban megértsük ezeknek a változásoknak az okait és hatásait a tollazat különböző funkcióira, további kísérletes vizsgálatokra van szükség. Eredményeim segítenek az egyik legjelentősebb globális környezeti hatás madarakra gyakorolt hatásainak megértésében és rámutatnak arra, hogy még vannak nagyon alulkutatott területek ebben a témában, melyek alapjául szolgálhatnak számos jövőbeli vizsgálatnak.

REZUMAT ÎN LIMBA ROMÂNĂ

În zilele noastre, urbanizarea este unul dintre cele mai puternice procese de transformare a habitatelor, care pune fauna sălbatică în fața a numeroase probleme. Mediul urban diferă în multe privințe de cel natural, cum ar fi hrana în cantitate și de calitate mai redusă, sau un microclimat mai cald, factori care pot influența în mod semnificativ succesul păsărilor care trăiesc în orașe.

În timpul studiilor mele de doctorat, am examinat efectele acestor factori de mediu modificați asupra succesului reproductiv și proprietăților penajului pițigoiului mare *(Parus major).* În cadrul unui experiment de manipulare a hranei efectuat pe teren, am demonstrat că lipsa hranei este principalul responsabil pentru succesul reproductiv mai scăzut, tipic păsărilor din orașe, și pentru dimensiunile corporale mai mici ale puilor, lucru bine cunoscut din literatura de specialitate: suplimentarea hranei puilor, în perioada de creștere a acestora, a condus la un succes reproductiv și dimensiuni corporale similare cu ale puilor din pădure. În schimb, în zonele de pădure nu a existat aproape niciun efect perceptibil al hranei puse de noi la dispoziție.

În alte două studii corelative am analizat modul în care mediul urban afectează numărul de pene ale păsărilor și proprietățile structurale ale fiecărui tip de pene. Examinând proprietățile structurale ale penelor, am găsit diferențe datorate habitatului în privința a numai câteva caracteristici, care au putut fi observate doar în primul an al păsărilor. Am arătat că penele de pe corpul păsărilor din orașe au în primul an o structură mai puțin densă decât ale celor din pădure, ceea ce poate contribui la o mai bună disipare a căldurii - sugerând un proces de adaptare la microclimatul urban mai cald. Mai mult, în primul an de viață al păsărilor am observat la penele aripilor și unele diferențe datorate habitatului, care însă pot indica mai degrabă efectele limitării hranei. Cu toate acestea, nu am constatat nicio diferență între păsările adulte, fapt care poate fi explicat prin capacitatea acestora de a asigura o termoreglare adecvată prin alte procese (de exemplu, prin suprafețe corporale nude și procese fiziologice), respectiv prin mortalitatea selectivă a păsărilor în primul lor an de viață, la care poate contribui în mod însemnat și calitatea mai slabă a penelor implicate în procesul de zbor.

Examinând și alte caracteristici ale penajului, am constatat și că puii de pițigoi din orașe au un număr mai mic de fulgi și pene de corp și o suprafață nudă mai mare, ceea ce contribuie la o mai bună disipare a căldurii, sugerând, de asemenea, adaptarea la microclimatul urban. Pentru a înțelege mai bine cauzele exacte ale acestor modificări și efectele asupra diferitelor funcții ale penajului, ar fi necesare studii experimentale suplimentare. Rezultatele mele contribuie la înțelegerea efectelor unuia dintre cele mai semnificative impacturi globale ale mediului asupra păsărilor și subliniază că în acest sens există încă domenii foarte puțin cercetate și care pot servi drept bază mai multor cercetări viitoare.

CHAPTER I.
GENERAL INTRODUCTION

Human population growth and socio-demographic factors are rapidly increasing the number and spatial extent of urban settlements across much of the globe (United Nations 2016). Although urban areas may maintain relatively diverse ecological communities, they typically support fewer species and lower diversity compared to surrounding semi-natural or natural landscapes (Aronson *et al.* 2014, Batáry *et al.* 2018), and this also contributes increasingly to the global extinction crisis (Mcdonald *et al.* 2008, Chaudhary *et al.* 2018). Furthermore, the rapid changes associated with urbanization could be strong drivers of evolutionary responses by wild animals and plants in cities, making urban habitats an ideal setting to study the adaptability of species to rapid ecological changes (Rivkin *et al.* 2019, Liker 2020). Improved understanding of both these adaptive changes and the factors that limit urban biodiversity is needed to devise urban management strategies that can enhance the species' existence, population sizes and well-being of animals in towns and cities, thus contributing to local and global conservation objectives (Ives *et al.* 2016, Lepczyk *et al.* 2017).

1.1. Food limitation in urban habitats

Urban animals are constrained by numerous factors including the spatial extent, composition and structure of vegetation, exposure to a range of pollutants (e.g. chemical, noise, heat; Isaksson 2010, Meillère *et al.* 2015b), human disturbance (Fernández-Juricic 2002), altered microclimate (see ***Chapter I,*** section *1.2. Urban heat island*) and, for some species, reduced availability of resources including food (Williams *et al.* 2009, Aronson *et al.* 2017, Moretto & Francis 2017). Due to the powerful landscape transformations, the altered vegetation composition (e.g. high proportion of alien species), and the use of pesticides and herbicides in urban areas, the arthropod communities have dramatically changed (e.g. Vergnes *et al.* 2012, New 2015) in cities. Although insects' responses to urbanization are diverse and taxon-specific, several studies have found that urban environments harbour a strongly reduced amount of insects (Jones & Leather 2012, New 2015, Fenoglio *et al.* 2020). In addition, Merckx *et al.* (2018) showed that urban insect communities are characterized by smaller species. Furthermore, it is also known that the carotenoid concentration of urban caterpillars is significantly lower than in forest ones. These habitat differences in insect communities result in a relative scarcity of high-quality food sources

(e.g. lepidopteran larvae; Narango *et al.* 2018, Seress *et al.* 2018, 2020, Jarrett *et al.* 2020) for insectivorous animals, like many bird species.

In contrast to the relative scarcity of natural food items, urban environments typically contain large amounts of anthropogenic food which are readily consumed by a range of species and can comprise a substantial proportion of the animals' diets (e.g. arthropods; Youngsteadt *et al.* 2016, birds; Robb *et al.* 2008, and mammalian carnivores; Bateman & Fleming 2012). These anthropogenic food sources, however, typically have lower nutritional quality than natural dietary components, and their consumption is often associated with adverse impacts on animals' physiology (e.g. Schulte-Hostedde *et al.* 2018), behaviour (Murray *et al.* 2015) and disease risk (Murray *et al.* 2016), and reproductive success (Mennechez & Clergeau 2006, Plummer *et al.* 2018). In combination, the abundant anthropogenic food sources and the scarcity of urban insects may drastically alter the quantity and quality of food for urban insectivorous animals, suggesting limited availability of high quality food during the most nutritionally demanding life-history stages, like reproduction, nestling development or feather growth of birds. These impacts have been particularly well studied in birds and, as predicted by the food limitation hypothesis, may contribute to the frequent (although not exclusive) pattern of lower reproductive success (e.g. fewer and smaller offspring; Peach *et al.* 2015, Pollock *et al.* 2017, smaller adult body size; Heiss *et al.* 2009, Meyrier *et al.* 2017, and altered growth curve, body mass and survival of nestlings; Corsini *et al.* 2021) in urban compared to non-urban avian populations. These effects may affect the survival chances of birds and their populations in cities (Minias *et al.* 2015, Podlaszczuk *et al.* 2016).

1.2. Urban heat island

Another important environmental factor in which cities differ from natural habitats is the altered microclimate. Cities are often characterized by higher ambient temperatures and drier microclimate compared to the surrounding non-urbanized areas (so-called urban heat island – UHI; Oke 1982, Arnfield 2003), which is mainly caused by elevated amounts of heat-absorbing and re-radiating surfaces, reduced vegetation cover, air pollutants and anthropogenic heat release (Rizwan *et al.* 2008). The maximal intensity of UHI can reach more than 10˚C in large cities (Tran *et al.* 2006, Chakraborty & Lee 2019), which can benefit urban wildlife by mitigating winter cold stress (Hinkel *et al.* 2003), but it can also pose significant challenges to them during the warm periods of the year. Besides the constant warmer microclimate in cities, the UHI may amplify the effects of extreme events caused by climate change, such as heat waves, by increasing

both the number and the intensity (causing up to 2.8°C higher difference compared to normal days; Zhao *et al.* 2018) of heat waves in cities (Ward *et al.* 2016, Pipoly *et al.* 2022). All of these effects are expected to intensify in the future, due to the combined effects of climate change, global human population growth and the increasing rate of urbanization (McCarthy *et al.* 2010, Zhao *et al.* 2021).

Although the number of studies examining the phenomenon of UHI has increased significantly over the past decade, we still know little about its effects on wildlife. The urban biota may respond to the UHI in numerous ways which in many cases can cause discrepancies at the community level as well. For example, in plants, it may induce temporal shifts in phenology, resulting in seasonally advanced flowering and prolonged vegetation period (reviewed by Jochner & Menzel 2015). However, the degree of phenological shifts may be highly different between species, resulting in phenological mismatches between them (Chick *et al.* 2019), and this may lead to disruptions in urban food chains, thus making foraging even more difficult for urban-dwelling species (Jochner & Menzel 2015, Zohner 2019). The effects of the UHI have already been documented in a wide range of animal species, negatively affecting the fitness and abundance of bees (Hamblin *et al.* 2018) and snail species (Baur & Baur 1993), and the body size of insects (Merckx *et al.* 2018) and birds (Pipoly *et al.* 2013). However, there are also examples of the UHI having neutral (e.g. on a shade-tolerant butterfly, *Pararge aegeria*) or even positive effects on some species, like on the larval survival and adult male body mass of a thermophilous butterfly (*Lasiommata megera;* Kaiser *et al.* 2016), development of Puerto Rican crested anole *(Anolis cristatellus)* hatchlings (Hall & Warner 2018), and the abundance of scale insects *(Parthenolecanium quercifex)* in warm urban areas (Meineke *et al.* 2013). Even more interestingly, several recent studies documented adaptive responses to elevated temperatures in some urban populations. For example, urban water fleas (*Daphnia magna*) and acorn ants (*Temnothorax curvispinosus*) acquired greater heat tolerance (Brans *et al.* 2017, Diamond *et al.* 2017) but for the latter species, this was also accompanied by a decrease in cold tolerance (Diamond *et al.* 2017).

Up to now, there have been relatively few studies examining the effects of UHI on birds. Based on these experimental and observational studies focusing on the effects of heat on the fitness of different bird species, we can expect some negative effects on urban birds. For example, high temperatures negatively affect the survival of nestlings in the nest (Conrey *et al.* 2016) and in the post-fledging period (Rodríguez *et al.* 2016) and also their body mass (Pipoly *et al.* 2013, Rodríguez *et al.* 2016, Andreasson *et al.* 2018). But on the other hand, we can also expect positive effects of UHI on birds. For example, the mitigating effect of UHI during cold spells in winter

(Hinkel *et al.* 2003) and even in the breeding season may increase the survival and the breeding success of urban birds. Furthermore, if urban birds become able to cope with constant urban heat (through thermal adaptations or phenotypic plasticity), they can either reduce or negate the effects of the warm climate. This is also suggested by the results of a recent long-term study in which Pipoly *et al.* (2022) showed that the survival of both urban and non-urban great tit nestlings (*Parus major*) was negatively correlated with the number of heat days, but this effect was much weaker in urban birds. Furthermore, they also found that while the body mass of forest nestlings is negatively affected by heat waves, these have less pronounced effects on the mass of urban nestlings. Overall, this study suggests that urban birds are less vulnerable to extremely hot weather than their non-urban counterparts.

To avoid overheating, birds use various physiological (reviewed by Ruuskanen *et al.* 2021), and behavioural thermoregulatory mechanisms (Kelly *et al.* 2004, Pattinson *et al.* 2020). However, all of these mechanisms have their costs and disadvantages, for example, changes in daily activities affect the foraging opportunities, and the provision rate of adult birds during the breeding season (Gardner et al. 2017), whereas panting may result in significant water loss (due to respiratory evaporative water loss; Smit *et al.* 2013). This latter could be compensated (especially in nestlings) by consuming high water content foods, like caterpillars, but these are known to be less available in urban habitats (Robb *et al.* 2008, Seress *et al.* 2018). Birds living in warm environments can, in turn, reduce the constant costs of active thermoregulation through adaptive physiological and morphological changes. A possible way for this in birds may be to evolve changes in plumage characteristics, which can, for example, promote their passive heat dissipation in warm environments.

1.3. Plumage - how can it be affected by urban habitats?

The plumage plays several vital roles in birds. It is essential for flying, waterproofing, insulation and displaying, thus plumage properties contribute to several fitness components (e.g. Swaddle et al. 1996, Echeverry-Galvis and Hau 2013, Minias et al. 2015). The structural quality of feathers and the density of the plumage (measured by the number of feathers per body surface area) vary among species (e.g. depending on the environment or flight type; Pap et al. 2015, 2017, Osváth et al. 2017), populations (Broggi *et al.* 2011, Gamero *et al.* 2015) or even among individuals (e.g. between age groups and sexes; Butler et al. 2008, De La Hera et al. 2010, Koskenpato et al. 2016). Note that adaptive changes in response to different environmental conditions can generate

between- and within-species differences both in the structural properties of feathers and the plumage density. Furthermore, the structural properties of feathers can change plastically to some degree from year to year (e.g. depending on the quality of available food; Murphy & King 1992, Pap *et al.* 2008, or the condition of birds; Vágási *et al.* 2012), while the density of plumage, more specifically the maximum number of feathers, is determined during embryonic development (e.g. determined by the conditions experienced by the egg-laying females and by the embryos during their development) and does not change after hatching (Yu *et al.* 2004, Dahlke *et al.* 2008, Scott *et al.* 2015).

Even though birds are amongst the most studied taxa in urban ecology, so far very few studies have explored how urban environments influence their feathers. One exception to this general lack of knowledge is plumage coloration. Several studies documented paler coloration in urban than in non-urban bird populations (Isaksson *et al.* 2006, Jones *et al.* 2010, Giraudeau *et al.* 2015, Biard *et al.* 2017, Grunst *et al.* 2020), which is presumably linked to the lower food quality and indirectly to the higher pollution in urban ecosystems (Eeva *et al.* 2009). There is very little or no information on the effect of urbanization on the structural properties of individual feathers and plumage density. The only study so far (Meillère *et al.* 2017) that examined the relationship between bird feather structure and urbanization showed that there is a negative correlation between tail feather density (feather mass/length ratio) and the degree of urbanization in juvenile house sparrows *(Passer domesticus).* Although this relationship was not shown in adult birds, which may indicate that the urban environment affects different age groups differently. However, the urban environment encompasses several environmental factors that can ultimately affect the structural characteristics of plumage.

One of the major changes birds have to face in urban environments is the lower quantity and quality of food sources (e.g. fewer invertebrates but abundant anthropogenic food; Jones & Leather 2012, Seress et al. 2018, Nadolski et al. 2021) and this may affect the plumage characteristics in two ways. First, the protein content of food is known to affect feather density in adult wild birds (Osváth *et al.* 2018), resulting in between-species differences (e.g. species feeding on plants usually have a lower plumage density than insectivorous species and birds of prey). Furthermore, it is also known from experiments in poultry that the food restriction of broilers during the egg-laying period determines the maximum number of feather follicles (thus the density of the plumage) in developing embryos (Scott *et al.* 2015), resulting in within-species differences. Second, because growing feathers is an energy and nutrient-demanding process (Lindström *et al.* 1993), the quality of the newly grown feathers is strongly affected by the individuals' physiological state and hence by the prevailing environmental conditions (e.g. food

availability) during this period. Several studies showed that food availability strongly affects the structural properties of feathers during the moulting period (e.g. Murphy & King 1992, Pap *et al.* 2008, Broggi *et al.* 2011), and very probably also during the nestling stage when the first feathers are being grown (Sillanpää *et al.* 2010). However, surprisingly (and contrarily to the plumage density effect mentioned above), the protein content of food consumed in adulthood by different species does not result in between-species differences in the structural properties of feathers (Pap *et al.* 2015, 2017).

Other environmental factors, like the altered microclimate of cities, may also affect both the plumage and feather density and the structural characteristics of feathers. For example, two recent comparative studies suggested a negative correlation between the ambient temperature of the species' environment and feather number (Møller 2015) and feather density (Osváth *et al.* 2018) in wild populations. However, much less is known about how these traits vary within a species. Two experimental works in captive poultry showed that the incubation temperature of eggs may affect the number of follicles formed in embryos (Dahlke *et al.* 2008, Scott *et al.* 2015). Furthermore, the altered microclimate may also affect the structural properties of feathers (especially on contour feathers that play role in insulation), but earlier studies reported conflicting results on these respects. For example, a within-species study found that contour feathers with denser insulating parts are adaptive in colder environments (Koskenpato *et al.* 2016), while a multispecies comparative study found a seemingly opposite pattern, i.e. that the feathers of bird species wintering in colder areas are less dense (Pap *et al.* 2017). The explanation of the authors for this latter result was that less dense plumage can be capable of trapping higher amounts of air near the body surface, thus enhancing the insulation capacity of the plumage (Pap *et al.* 2017). In sum, these conflicting conclusions of the earlier studies make it difficult to predict how environmental temperature influences feather properties in a particular species, and call for further studies.

CHAPTER II.
THESIS OBJECTIVES

During my doctoral studies, I focused on two main topics, both of which are integral parts of current research on the effects of urbanization on wild populations. First, in a controlled food manipulation experiment, I studied one of the most fundamental impacts of the urban environment: the effects of food limitation on the reproductive success of birds. Second, I examined the effects of the urban environment on plumage characteristics, in which, in addition to constraints due to food limitation, adaptation to the altered urban microclimate may also play a crucial role.

Specifically, my aim was to answer the following questions:

1. How does the food limitation of the urban environment affect the reproductive success of urban birds?
2. Is there any difference in the structure of contour feathers between urban and forest birds?
3. Is there any difference in the structure of flight feathers between urban and forest birds?
4. Is there any difference in the number of feathers and the density of plumage in the ventral feather tracts between urban and forest birds?

I will explore these questions in three studies conducted between 2016-2018 by the members of the Behavioural Ecology Research Group, University of Pannonia (currently ELKH-PE Evolutionary Ecology Research Group). In the study presented in ***Chapter IV*** I participated in study design, field data collection, data preparation and writing of the manuscript. In studies presented in ***Chapter V*** and ***Chapter VI*** I was the lead author in all stages of the studies from their conceptualization to the writing of manuscript.

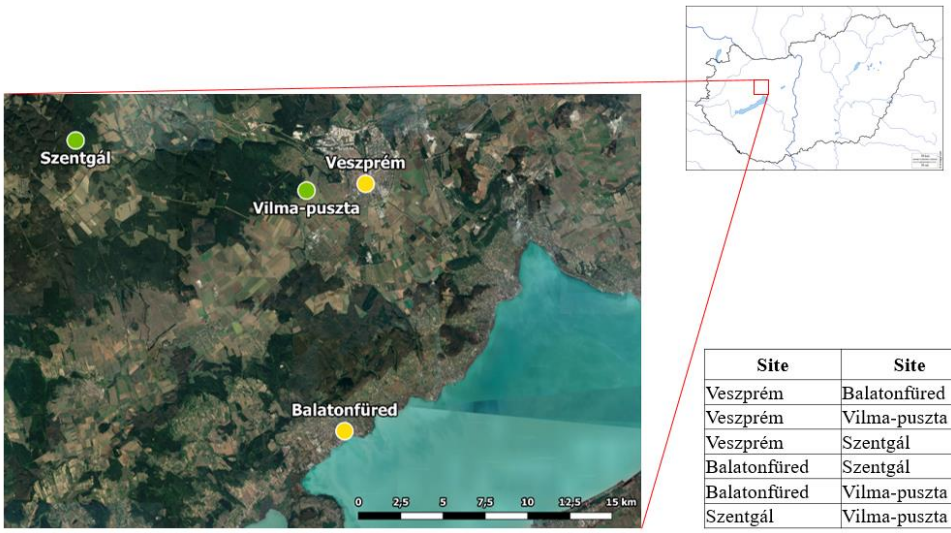
CHAPTER III.
GENERAL METHODS

As a model organism, we studied the great tits, a small insectivorous passerine species common in urban and natural habitats across the Western Palearctic (Gosler & Clement 2007). Its populations are non-migratory in our study region (Csörgő & Török 2009), and individuals are thus affected by local factors (food availability, temperature) across all of their annual cycle.

Our studies were conducted in four study sites (in two urban and two forest sites) located in Veszprém County, Hungary. In the two urban study sites (Balatonfüred 46°57'30.82" N, 17°53'34.47" E and Veszprém 47°05'17.29" N, 17°54'29.66" E, located 14 km from each other; Figure III.1.) the nestboxes were placed in university campuses, public parks, and a cemetery, that are surrounded by built-up areas and roads and experience frequent anthropogenic disturbance. The vegetation of these sites consists of both native and introduced plant species. One of the forest study sites (near the village of Szentgál, 47°06'039.75" N, 17°41'017.94" E) is a deciduous woodland characterized mainly by European beech *(Fagus sylvatica)* and European hornbeam *(Carpinus betulus)*. The other forest site is at Vilma-puszta, located c. 14 km away from Szentgál forest and 3 km from the edge of the closest urban study site, Veszprém. Vilma-puszta is a mature deciduous woodland characterized mainly by downy oak *(Quercus cerris)* and South European flowering ash (*Fraxinus ornus*; 47°05'06.7"N, 17°51'51.4"E). This latter study location is a Natura 2000 site that is relatively free from human disturbance, e.g. it has no paved roads, has only one nearby farm and no logging activity. Great tits are resident birds in all study sites and bred in the nestboxes since 2013. Ringing data indicate limited dispersal between the urban and rural study sites (one recorded instance from over 1,100 re-trapping or re-sighting observations of c. 4,100 individually marked birds between 2011 and 2019).

In our earlier studies, we have shown that these study sites differ in many aspects. For example, the degree of urbanization highly differs between the sites as reflected by their urbanization scores measured by the 'UrbanizationScore' software (Seress *et al.* 2014). Furthermore, it has been shown that the amount of high-quality arthropod food (caterpillars) during the breeding season is significantly (8.5-24 times) lower in urban sites (Seress *et al.* 2018), and this food limitation is also reflected in nestlings' food composition (Sinkovics *et al.* 2021) and has a strong negative impact on nestling development and survival (Seress et al. 2020). In addition, Pipoly *et al.* (2022) revealed that during the nestling period (from the earliest hatching date to the latest nestling ringing date between 2013 and 2018 in these four study sites), the

temperature in these urban sites were significantly warmer compared to forest sites (urban-forest difference, *mean* ± *SE*: 1.52 ± 0.27 °C). Furthermore, they also counted the occurrence of heat days during the 6 year nestling period. They defined the heat days at the 90% percentile of all daily maximum temperatures from a 26-years long temperature dataset measured near Veszprém, which was 28.7°C. Pipoly *et al.* (2022) showed that during the nestling period, the number of heat days was 2.7 times higher in urban areas than in the forest sites (urban-forest difference: 0.99 ± 0.13 days).



Site	Site	Distance (km)
Veszprém	Balatonfüred	14
Veszprém	Vilma-puszta	3
Veszprém	Szentgál	17
Balatonfüred	Szentgál	23
Balatonfüred	Vilma-puszta	14
Szentgál	Vilma-puszta	14

Figure III.1. The location of the two urban (Veszprém and Balatonfüred; yellow) and the two forest (Vilma-puszta and Szentgál; green) sites in Hungary, and the distances between their middle points (table).

CHAPTER IV.
FOOD AVAILABILITY LIMITS AVIAN REPRODUCTION IN THE CITY: AN EXPERIMENTAL STUDY ON GREAT TITS

Abstract

The altered ecological and environmental conditions in towns and cities strongly affect demographic traits of urban animal populations, for example, avian reproductive success is often reduced. Previous work suggests that this is partly driven by low insect availability during the breeding season, but robust experimental evidence that supports this food limitation hypothesis is not yet available. In this study, we tested core predictions of the food limitation hypothesis using a controlled experiment that provided supplementary insect food (nutritionally enhanced mealworms supplied daily to meet 40-50% of each supplemented brood's food requirements) to great tit nestlings in urban and forest habitats. Furthermore, we measured parental provisioning rates and estimated the amount of supplementary food consumed by control and experimental nestlings, and assessed their body size and survival rates. We found that the provisioning rates were similar across habitats and control and supplemented broods, but supplemented (and not control) broods consumed large quantities of supplementary food. As predicted by the food limitation hypothesis we found that nestlings in (1) urban control broods had smaller body size and nestling survival rates than those in forest control broods, (2) forest supplemented and control broods had similar body size and survival rates, (3) urban supplemented nestlings had larger body size and survival rates than those in urban control broods, and crucially (4) urban supplemented broods had similar body size and survival rates to nestlings in forest control broods. Our results provide rare experimental support for the strong negative effects of food limitation during the nestling rearing period on urban birds' breeding success in our study system. Furthermore, the fact that supplementary food removed or considerably reduced habitat differences in survival rate and nestling body size suggests that urban stressors other than food shortage contributed relatively little to the reduced avian breeding success. Finally, given the impacts of the amount of supplementary food that we provided and taking clutch size differences into account, our results suggest that urban insect populations in our study system would need to be increased by a factor of at least 2.5 for urban and forest great tits to have similar reproductive success.

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4.1. Introduction

Food supplementation experiments are widely used in avian ecological research, and constitute a key approach to test the food limitation hypothesis in ecological studies. Studies manipulating nestling food quantity and/or quality in urban environments are rare and have produced inconsistent evidence for a link between food limitation and reduced breeding success. One experiment (Bańbura *et al.* 2011) on urban great tits reported positive effects of extra food on some traits (nestling body size and blood heterophil-to-lymphocyte ratio) but not on others (several other blood parameters) – although in this study the extent to which focal parents and their nestlings used the extra food is unclear. Other food supplementation experiments on urban birds have found negligible (Meyrier *et al.* 2017) or even negative (Demeyrier *et al.* 2017) impacts on body size and/or nestling survival. We are aware of only two studies that compared the effects of food supplementation between urban and non-urban populations of the same species. Supplementary food had similar positive effects on house sparrows' nestling survival and number of fledglings in suburban and rural gardens, suggesting that the suburban sparrows were not more food-limited than the rural birds (Peach *et al.* 2014). This study, however, did not control for the confounding effects of brood size, nestling age and the amount of supplementary food obtained by different broods. A study on American crows *(Corvus brachyrhynchos)* found larger body size in urban supplemented nests, whilst in rural areas supplementary food reduced body size, but the study was limited by extremely small sample sizes with a total of just 7 supplemented nests (Heiss *et al.* 2009). These studies, with the exception of Bańbura *et al.* (2011), also provided no information on the amount of natural food in the urban and rural study systems and thus the potential magnitude of food shortage experienced by the focal urban bird populations. There is thus a need for additional tests of the urban food limitation hypothesis that build upon earlier work by conducting food supplementation experiments across urban and rural populations using larger sample sizes, quantifying the use of supplementary food by target individuals, placing this in the context of the difference in natural food availability of urban and rural bird populations, and assessing the influence of a wider range of potentially confounding variables on metrics of avian reproductive success.

In a recent study, we showed that lower breeding success of urban great tits is primarily driven by increased nestling mortality, for which starvation was the most likely explanation (Seress *et al.* 2018). Here, we build upon this finding and experimentally test the food limitation hypothesis using a food supplementation experiment in urban and forest populations. We regularly provisioned extra insect food throughout the brood-rearing period to manipulate

nestlings' diet, and compared parental provisioning behaviour, nestling body size and survival between supplemented (treatment) and non-supplemented (control) broods within and between habitat types. We predicted that (1) control broods in the urban habitat would have reduced provisioning rates, nestling body size and survival compared to control broods in forest, indicating that food availability during the nestling phase limits breeding success in urban but not in forest areas, and thus (2) control and supplementary fed broods in forested locations would exhibit negligible differences in provisioning rate, body size, and nestling survival, whilst (3) urban supplemented broods would have significantly increased provisioning rates, nestling body size and survival compared to urban control broods. Finally, if food limitation is indeed a major factor limiting breeding success and nestling development in cities, we expect to find that (4) extra insect food would eliminate or considerably mitigate the differences in reproductive success between urban supplemented and forest control groups.

4.2. Methods

4.2.1. Data collection and experimental design

We studied great tits breeding in nestboxes at an urban (Veszprém) and a forest site (Vilma-puszta) in 2017 (for a detailed description of study sites see ***Chapter III***). To test the food limitation hypothesis, we manipulated nestlings' diet in a field experiment, in which great tit broods were allocated to a food supplementation treatment (treatment group) or received no extra food (control group). We monitored nestboxes at least twice a week from 1st March to early June to record laying and hatching dates, and the number of eggs and nestlings in active great tits nests. At each study site, we randomly assigned the first brood of the season to the supplemented or control group, and then sequentially allocated each additional brood to the supplemented or control groups to ensure similar sample sizes in each group and to avoid the potential for treatment type to be confounded with date. The experiment only included first broods (we identified parent birds by their unique colour ring combinations applied to them in previous years, or based on their plumage characteristics). During the incubation period, we equipped all nestboxes with a feeder box, which was a small (125 ml) plastic container attached to the nestbox a few centimetres below the entrance (Figure IV.1). This proximity to the nestbox helped focal birds to defend the supplementary food from non-target individuals, which was further facilitated by using opaque feeder boxes to decrease the conspicuousness of mealworms to other birds (use of mealworms by non-target individuals was very rare, see ***Chapter IV,*** section *4.3. Results*). The bottom of the feeder boxes had small holes (1 mm diameter) that enabled rainwater drainage but

did not allow supplementary food (mealworms) to escape. Control and supplemented nests were not clustered within separate parts of the study sites, and the mean distance (± *SE*) between the nearest neighbouring control and supplemented broods were 98 ± 12 m (range: 37-211 m) in the urban site, and 67 ± 8 m (31-112 m) in the forest site.



Figure IV.1. Nestbox with a plastic feeder box attached below the entrance hole, with some mealworms in it. The black plastic box attached to the right serves for concealment for the video camera (see Seress *et al.*, 2017).

Treatment broods received supplementary food on a daily basis when nestlings were 3-15 days old (hatching day of the first egg = day 1). This ensured that food supplementation did not influence reproductive success by altering clutch sizes or the body condition of incubating females. We adjusted the amount of mealworms according to brood size and nestling age by providing 1.5 g/chick/day between 3-7 days of nestling age (i.e., for 5 days), and 3 g/chick/day between 8-15 days of nestling age (i.e., for 8 days). Thus, a brood with 10 nestlings received daily c. 120 and 240 larvae in the early and late nestling rearing phases, respectively. These quantities are estimated to cover 40-50% of daily food requirements of great tit nestlings (Gibb and Bets 1964, Van Balen 1973, our own unpublished data). Mealworms are widely used in avian food supplementation experiments (Bańbura *et al.* 2011, Peach *et al.* 2014, Demeyrier *et al.* 2017), and are suggested to be a good source of energy and digestible amino acids for birds (Finke 2002). To increase the nutritional value of mealworms we transferred the larvae from their usual wheat bran substrate to an *ad libitum* invertebrate food substrate rich in protein and vitamins (www.bugs-world.com, product code: BW-TT), at least 2-3 days before being provided to birds (for similar approach see e.g. Kaiser *et al.* 2014). Daily food supplementation occurred between 8:00 and 13:00, and during these visits we also recorded the number of chicks (alive or

dead) in the nest, which enabled us to calculate the required amount of supplementary food for each brood. To avoid inducing nest desertion, we never removed brooding parents during these checks – thus, if a parent remained on the nest during nest inspection we used the most recent data on brood size to calculate the required amount of supplementary food. Feeding boxes were cleaned daily and leftover food was weighed (to the nearest g). Control broods did not receive supplementary food but their nests were also checked daily and we spent a similar amount of time (c. 3-4 minutes) at the nest during each visit to ensure that control and supplemented broods received the same level of human disturbance.

When nestlings reached 15-days of age (i.e., just before fledging) we ringed and weighed them (± 0.1 g) and also measured the length of the left tarsus (± 0.1 mm) and right wing (± 1 mm; from the bend of the wing to the tip of the longest primary, following the 'flattened and straightened wing' method; Svensson, 1992). In the supplemented group a few hours had always passed between the most recent provision of supplementary food and the measurements (4.68 ± 0.14 h) in order to let the birds digest the supplementary food. None of the nestlings from the nests included in the study fledged before the age of 15 days.

The experiment involved 52 broods initially, but due to complete breeding failure resulting from nest desertion during the incubation or early chick-rearing period (which is usually due to parental death; Santema & Kempenaers 2018), we excluded five nests (n = 3 urban control, n = 1 urban supplemented, n = 1 forest supplemented). Thus final sample sizes were: urban control broods 10, urban supplemented broods 14; forest control broods 12 and forest supplemented broods 11 (Table S.IV.1.).

Frass sampling of the dominant tree species at each site demonstrated that, as was the case in previous years, caterpillar abundance was higher in the forest compared to the urban site in 2017 (Figure S.IV.1**;** Seress *et al.* 2018). Breeding success of urban and forest pairs that did not receive supplementary food was comparable to that reported between 2013-2016 from the same study sites (Seress *et al.* 2018; Table S.IV.1-2). Thus, it can be concluded that although this current study was conducted in a single year and two study sites (one forest and one urban), its data likely represent the main characteristics of our study system, providing generalizable results within this system.

During the experiment there was, however, a brief unusual cold spell from 18th-21st April 2017 with occasional snowfall and low ambient temperatures (Glądalski *et al.*, 2018; see more details and analyses in Appendix *A/I.1 Coldspell*). During this period most urban nests already contained recently hatched nestlings whilst forest clutches were still being incubated (reflecting

the typical trend for earlier laying in urban sites, see Seress *et al.* 2018). This adverse weather might have disproportionately affected the early development of urban nestlings. However, the exposure to the cold spell did not have a significant interaction with the treatment in models of any of our response variables, and control urban nestlings that experienced the cold spell did not have smaller body mass than non-manipulated broods from the same urban site from other years with normal weather conditions (Appendix *A/I.1 Coldspell*). Thus, we conclude that it is highly unlikely that the exposure of urban broods to the cold spell biased the effects of the supplementary food treatment.

4.2.2. Behavioural data collection

Small video cameras (HD Hero, GoPro) mounted in a non-transparent plastic box for camouflage (c. 15 cm from the feeder) were used to monitor use of the feeder and parental provisioning behaviour (Seress *et al.* 2017). Videos (60 minutes duration) were recorded when chicks were 3-5 days old (*mean* ± *SE*, supplemented group: 4.1 ± 0.3 d, control group: 4.3 ± 0.1 d) and 9-11 days old (supplemented group: 9.9 ± 0.1 d, control group: 10.0 ± 0.1 d). Due to logistical constraints videos (n = 67) were obtained for 42 broods (number of broods: forest control / supplemented: 11 / 10, urban control / supplemented: 8 / 13), of which 25 were recorded at both chick ages, and 17 broods were only recorded when chicks were 9-11 days old. Videos were only taken during favourable weather conditions (i.e. not during heavy rain or strong winds) during the morning or early afternoon (urban: 09:00-14:30, forest: 10:00-15:30).

From each video, we extracted data on food provisioning rates (calculated per nestling). For supplemented broods we also categorized food items into three food types: mealworm, non-supplementary food (mainly caterpillars and other arthropods), or unidentified food item (8 of the 1526 feeding events). We recorded if birds (of any species) other than the focal brood's parents took supplementary food from the feeder (parents could be identified by unique colour ring combinations (66 of the 84 focal parents) or unique plumage marks (e.g. width of the breast stripe and overall colouration; the remaining 18 parents). We never captured and ringed adults or measured nestlings before video recording to avoid possible disturbances to birds' behaviour (Seress *et al.* 2017). Finally, we also recorded if parents consumed supplementary food themselves (through either direct capture of the feeding event on the video or by assuming self-consumption if a parent took supplementary food but did not deliver it to nestlings on its subsequent visit to the nestbox).

4.2.3. Statistical analysis

We conducted three analyses to further investigate how parents used the supplementary food. First, we tested if urban and forest supplemented birds utilized the same proportion of the supplementary food that was provided during the entire nestling period and compared habitats using a Mann-Whitney test (data distributions did not permit parametric tests). Second, we calculated the proportion of mealworm prey in the nestling diet to investigate how much urban and forest parents supplemented their nestlings' diet with mealworms. We fitted a linear mixed model (*LME*, package *'nlme'*) in which the response variable was the ratio of mealworms across all prey items (the number of mealworms divided by the number of all food items; $n = 8$ unidentified food items were excluded), and predictors were habitat, time of the day (number of minutes from 6:00 a.m. until the start of the video recording), nestling age and brood size. Note that as videos were recorded during the same short nestling age periods (3-5 and 9-11 days post-hatch), we included nestling age as a binary variable with these two age categories. We included brood ID as random factor to control for the non-independence of two video recordings on the same broods. Third, we also calculated the proportion of mealworms consumed by parents, and compared this ratio between habitats. We built a generalized linear mixed-effects model with quasi-binomial error distribution (*glmmPQL*, package *'MASS'*), in which the response variable was the ratio of mealworms consumed by the parents (number of consumed mealworms divided by the number of all utilized mealworms), and predictors were habitat, time of the day, nestling age (two-level factor) and brood size; brood ID was a random factor. From this latter analysis we excluded one video recording (an urban brood) because the parents did not consume or provision any mealworms during the 60-min video so we could not calculate this ratio (although field observation and the usually zero amount of leftover food in the feeder confirmed that these parents usually utilized the supplementary food).

To test our specific predictions for the effects of food supplementation treatment on reproductive success (outlined in the ***Chapter IV,*** section *4.1. Introduction*) we followed the approach suggested by Ruxton & Beauchamp (2008) and applied pre-planned pairwise comparisons between specific groups of habitat and treatment combinations of interest, as this method is a powerful approach for testing a priori hypotheses. We conducted the comparisons in two steps: first, we built separate linear models for nestling body size traits, survival rate and nestling provisioning rate and used these models to identify significant confounding variables besides the effects of treatment and habitat. Second, following the specific guidance of Ruxton

& Beauchamp (2008) we conduct all the pre-planned comparisons (regardless of the results of the first stage analysis) and calculated linear contrasts between specific groups of habitat and treatment combinations from linear models that also contained the confounding variables that had significant effects. These steps are described in detail below.

First, we fitted separate LME models for nestling' body mass, tarsus length and wing length (all measured at day 15). In these three models, predictors were food supplementation treatment (supplemented or control), habitat, treatment × habitat interaction, brood size, and time of day when modelling body mass. We used brood ID as a random factor in all these models. We also included date (number of days elapsed from the 1st of January until the measurement) in these models, but because forest great tits laid on average 7-8 days later than their urban conspecifics (Seress *et al.* 2018), we found a moderate level of collinearity between habitat type and date (variance inflation factor (*VIF*) > 3.26 in all cases, i.e. above the threshold above which collinearity is a concern (Zuur *et al.* 2010); using function *'vif'* from package *'car'*). Thus, to reduce multicollinearity we mean-centered the date separately for urban and forest broods and used this transformed variable in the models.

The food limitation hypothesis predicts lower nestling survival due to starvation in urban areas. Thus, we calculated the proportion of nestlings surviving from day 3 to day 15 (i.e., from the start of the experiment until ringing) and built a generalized linear model (GLM) with binomial error distribution, logit link function. In this model, the response variable was the proportion of nestlings surviving (i.e. the unit of analysis was individual broods and thus we did not include brood identity as a random factor), and predictors were treatment, habitat, treatment × habitat interaction, mean-centred date and brood size. Because in the forest supplemented group survival rate was 1.00 (i.e., all nestlings survived), we applied Firth logistic regression (using package *'brglm'*) to handle the problem of separation.

We also analysed the provisioning rates of parents in an LME model in which the response variable was provisioning rate (transformed as $\log_e(x + 0.5)$), and predictors were treatment, habitat, treatment × habitat, mean-centred date, time of the day and nestling age (two-level factor); random factor was brood ID. We were unable to include potential confounding effects of parental age, a possible proxy for experience, because this would have reduced sample sizes by between 11 and 30% for each comparison group – generating an unhelpful reduction in statistical power. Consideration of the age of parents for which data were available strongly suggests, however, that our results and inference are not biased by variation in parental age across

our four groups of birds (urban control, urban supplemented, forest control and forest supplemented; Table S.IV.3). We report the results for all full models in Table S.IV.4).

In the second step, we used separate linear models to compare the means of the response variables (i.e., the three nestling body size traits, survival rate and nestling provisioning rate) between specific habitat-treatment combinations. These models always contained the habitat × treatment term, plus any other confounding variable that was significant in the above described models (Table S.IV.4), specifically: date in the tarsus length and survival rate models, and nestling age (as two-level factor) in the nestling provisioning rate model; the random factor was brood ID (except for the model on nestling survival). We calculated linear contrasts between groups and used function *'glht'* (in package *'multcomp'*) to test whether these contrast differed from zero after applying the false discovery rate (fdr) method for correcting *P*-values for multiple pairwise comparisons. Specifically, we compared the means of the above five response variables in the following group pairs: (1) forest control vs. urban control (to confirm the effect of habitat on control broods); (2) forest control vs. forest supplemented and (3) urban control vs. urban supplemented (to test for the effects of supplementary food within habitat types); and finally, (4) forest control vs. urban supplemented (to test whether the food-supplementation was sufficient to eliminate or considerably mitigate differences between habitats).

To aid the interpretation of nestling survival analyses, we calculated survival probabilities of nestlings in the four groups from the model's parameter estimates. We used the same GLM as in the linear contrast analysis (see above) and transformed the habitat-treatment group mean estimates (*b*, provided on a logit scale) of the proportion of survived nestlings to survival probabilities *(p)* using the formula: $p = \exp(b) / (1 + \exp(b))$ (Zuur *et al.* 2009) – this is referred to as the survival probability in the rest of the manuscript.

All analyses were conducted in R (v. 3.5.2, R Core Team). We checked the validity of statistical assumptions for each linear model described above (Zuur *et al.* 2009), and the calculated VIF values for all our models (*VIF* 2.55) were below the threshold at which results are influenced by collinearity (Zuur *et al.* 2010). We define the two-tailed statistical significance level at $p < 0.05$.

4.3. Results

4.3.1. Acceptance of supplementary food and provisioning behaviour of the parents

Videos showed that birds in both habitats used most of the supplementary food, and we found no significant difference in the ratio of the amount of leftover food between urban (1.4%) and forest (4.2%) supplemented nests (Mann-Whitney, $n = 25$, $W = 66$, $p = 0.542$). Videos also revealed that birds other than the nest owners occasionally visited the nestboxes both in the control and in the supplemented groups. Species that visited the nestboxes (in control and supplemented groups combined) included great tits (7 cases), great spotted woodpeckers (*Dendrocopos major*, 3 cases), collared flycatchers *(Ficedula albicollis,* 2 cases), tree sparrows *(Passer montanus,* 2 cases) and a blue tit (*Cyanestes caeruleus).* Visitor birds appeared on 16.7% (5 out of the 30) of the control videos, and on 24.3% (9 out of 37) of the supplemented videos, stealing mealworms from the feeders in 6 out of the 9 videos. However, on these 6 videos (5 urban, 1 forest), the amount of food stolen (57 mealworms in total, *mean* ± *SE*: 8.14 ± 3.12 per video) was small compared to the amounts utilized by the focal parents (390 mealworms, 55.71 ± 11.14; paired-test, $t_6 = 3.72$, $p = 0.009$). Visiting great tits (all in the urban habitat) may have largely comprised of floaters and were either not ringed, or were ringed but not included in the experiment, except one urban male that was the parent of a neighbouring supplemented brood. We did not record any great tits from the control group stealing supplementary food from the feeders on supplemented nestboxes.

In supplemented nests we found that parents readily fed their chicks with the supplementary food, as the proportion of mealworms in nestlings' diet was 81.1% in urban and 75.3% in forest broods, but neither habitat type (LME, $b \pm SE$: 0.02 ± 0.09, $t_{21} = 0.192$, $p = 0.849$), nor any other predictor had significant influence on the proportion of mealworm in the diet of supplemented nestlings ($p > 0.351$ in all cases). Investigating the proportion of mealworms that parents consumed, we found a marginally non-significant habitat effect (GLM, $b \pm SE$: 0.55 ± 0.31, $t_{20} = 1.77$, $p = 0.093$), with urban parents tending to consume more mealworms (24.7%) than forest parents (18.1%). We also found a significant effect of nestling age, as parents consumed more extra food themselves when they were raising younger nestlings (3-5 days old) compared to when they were provisioning older chicks (9-11 days) (GLM, $b \pm SE$: -0.80 ± 0.28, $t_{13} = -2.83$, $p = 0.014$).

Nestling provisioning rate was similar between treatment groups and habitats, and none of the four pre-planned pairwise comparisons revealed significant differences between groups

(Table IV.1a). Provisioning rate was significantly higher in the 9-11 day compared to the 3-5 day old age category (Table S.IV.4).

4.3.2. Nestling body size

The results of the pre-planned pairwise comparisons for body mass, wing and tarsus lengths confirmed that (1) forest control nestlings were significantly larger than urban control nestlings for all three body size metrics (Figure IV.1a-c, Table IV.1b-d). In line with our expectations, we found that (2) forest control and forest supplemented groups did not differ significantly in any variables, whereas (3) supplementary feeding significantly increased body mass, wing and tarsus lengths in urban supplemented nestlings compared to the control group (Figure IV.1a-c, Table IV.1b-d). Finally, (4) supplementary feeding removed or considerably reduced the differences in body mass, wing and tarsus lengths that occurred between control forest and urban broods (Figure IV.1a-c, Table IV.1b-d). Although the difference between forest control and urban supplemented groups was close to statistical significance in body mass (Table IV.1b) and was statistically significant in wing length (Table IV.1c), the magnitude of these differences were small (body mass (g): 0.90 ± 0.46, wing length (mm): 3.58 ± 1.58).

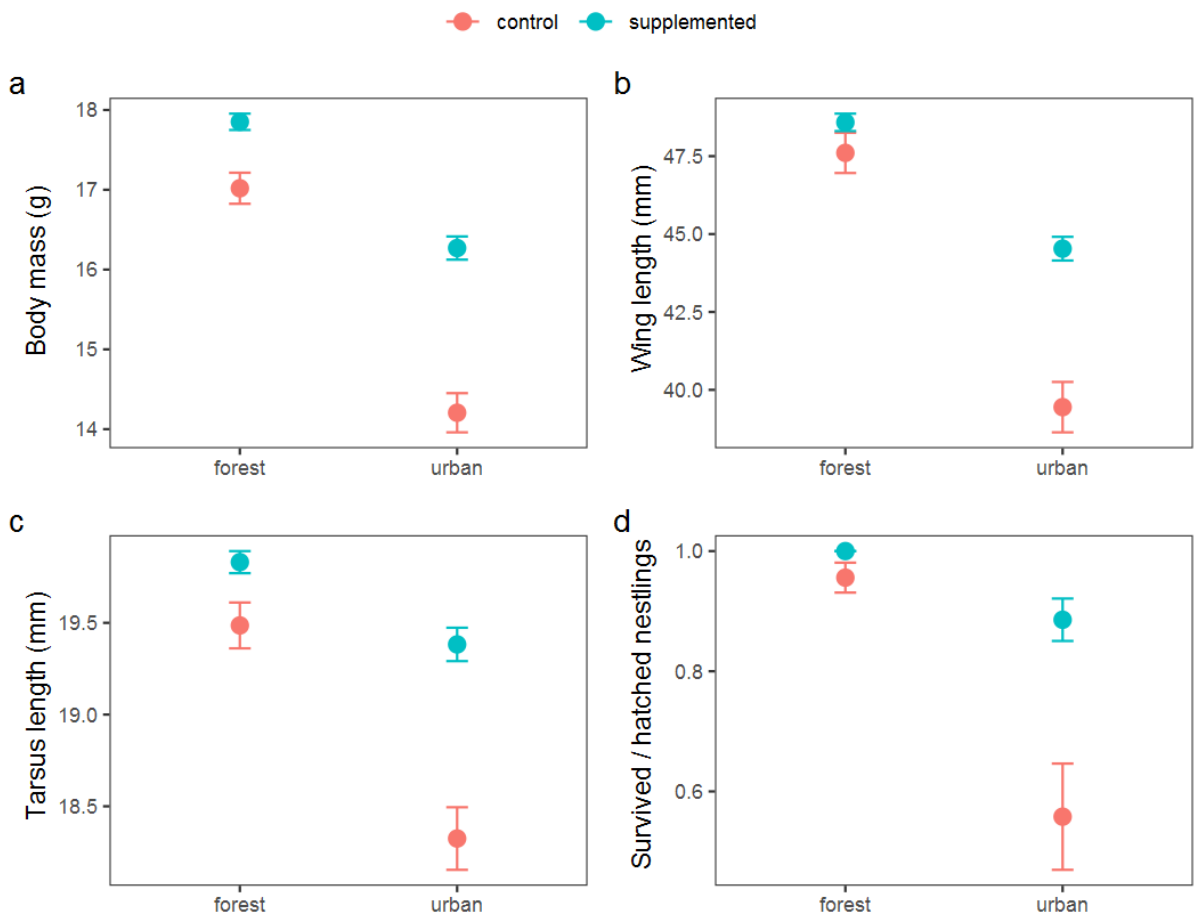


Figure IV.1. Differences (*means* ± *SE*) in 15-days old great tit nestlings' (a) body mass, (b) wing length, (c) tarsus length, and (d) in nestling survival in the groups of different habitat × treatment combinations.

4.3.3. Nestling survival

Nestling survival probabilities (p), estimated from the GLM model, were 1.00 and 0.95 in forest supplemented and control broods, respectively, while this was 0.88 in the urban supplemented and only 0.58 in urban control broods. The pre-planned pairwise comparisons indicated (1) significant differences in nestling survival probabilities between forest control and urban control groups (Table IV.1e; Figure IV.1d). (2) The difference in survival probability between forest supplemented and forest control groups was close to statistical significance but remained slight, whereas (3) survival was significantly and considerably higher in the urban supplemented compared to the urban control groups (Table IV.1e; Figure IV.1d). Finally, (4) whilst we found that the difference in survival probability between the forest control and urban supplemented groups was close to statistical difference its magnitude was small; Table IV.1e; Figure IV.1d).

Table IV.1. The results of the pre-planned pairwise comparisons showing the differences in (a) great tit parents' provisioning rates (log-transformed using the formula $\log_e(x+0.5)$, and in their nestlings' (b-d) body size and (e) proportion of survived nestlings (on a logit scale) between groups of treatment × habitat combinations. The linear contrasts between groups were calculated from linear models (LME for a-d, and

GLM for e), containing the habitat × treatment interaction, plus any confounding variable that was proven to be significant in the full model (Table S.IV.4). Statistically significant ($p < 0.05$) differences are highlighted in bold and marginally non-significant ($0.05 < p < 0.10$) differences are shown in italic.

Pairwise comparisons	*contrast ± SE*	*z*	*adjusted p-value*
(a) Provisioning rate (feeding/nestling/hour) [1]			
forest control – urban control	0.20 ± 0.21	0.94	0.654
forest control – forest supplemented	-0.09 ± 0.20	-0.45	0.654
urban control – urban supplemented	-0.31 ± 0.20	-1.53	0.502
forest control – urban supplemented	-0.12 ± 0.17	-0.66	0.654
(b) Nestling body mass (g; day 15) [2]			
forest control – urban control	2.90 ± 0.52	5.54	**< 0.001**
forest control – forest supplemented	-0.78 ± 0.48	-1.61	0.107
urban control – urban supplemented	-2.00 ± 0.51	-3.92	**< 0.001**
forest control – urban supplemented	0.90 ± 0.46	1.97	*0.066*
(c) Nestling wing length (mm; day 15) [2]			
forest control – urban control	9.13 ± 1.79	44326	**< 0.001**
forest control – forest supplemented	-0.73 ± 1.66	-0.44	0.662
urban control – urban supplemented	-5.55 ± 1.74	-3.19	**0.003**
forest control – urban supplemented	3.58 ± 1.58	44254	**0.031**
(d) Nestling tarsus length (mm; day 15)[2]			
forest control – urban control	1.25 ± 0.35	3.59	**0.001**
forest control – forest supplemented	-0.34 ± 0.31	-1.12	0.348
urban control – urban supplemented	-1.06 ± 0.34	-3.09	**0.004**
forest control – urban supplemented	0.19 ± 0.29	0.66	0.512
(e) Nestling survival (between day 3-15) [3]			
forest control – urban control	2.67 ± 0.50	5.33	**< 0.001**
forest control – forest supplemented	-2.48 ± 1.49	-1.67	*0.096*
urban control – urban supplemented	-1.68 ± 0.37	-4.49	**< 0.001**
forest control – urban supplemented	0.99 ± 0.53	1.86	*0.084*

[1] Number of broods (control/supplemented): urban: 8/13, forest: 11/10

[2] Number of nestlings (nr. of broods; control/supplemented): urban: 45 (9)/96 (14), forest: 99 (12)/104 (11)

[3] Number of broods (control/supplemented): urban: 10/14, forest: 12/11

4.4. Discussion

Urbanisation can be associated with adverse impacts on demographic traits (Sepp *et al.* 2018), and these impacts probably contribute to the reduced biodiversity of towns and cities (Aronson *et al.* 2014). The mechanisms driving reduced demographic success in urban environments are, however, poorly understood (Rodewald & Gehrt 2014). In this study we used a food supplementation experiment, using mealworms fed on an enriched diet, to test if the reduced

abundance of insect food sources in urban environments (e.g. Seress *et al.* 2018) explains reduced reproductive success and smaller nestling size in an insectivorous bird.

As predicted by the food limitation hypothesis, control broods that did not receive supplementary food were smaller and had lower survival rates in the urban site than the forest site – matching previous studies of reproductive success in unmanipulated great tit populations (Bailly *et al.* 2016, de Satgé *et al.* 2019) including our focal study populations (Seress *et al.* 2018). Crucially, urban supplemented broods had considerably higher fledging success and produced larger nestlings than urban control pairs, whereas supplementary feeding of forest broods had only small and statistically non-significant effects on these traits. Furthermore, supplementary fed urban broods had similar body sizes and survival rates to those of control broods in the forest environment. Collectively, these results provide rare and strong experimental evidence that the negative impacts of urbanization on avian nestling size and survival is caused by the reduced availability of high-quality invertebrate food sources, and these effects can be mitigated by providing arthropod-based supplementary food. Our experiment suggests that food limitation can strongly influence even successful urban adapter species such as the great tit, which across its range is one of the commonest birds in towns and cities (Gosler & Clement 2007). The very small differences in nestling size and survival between urban supplemented and forest control chicks suggest that food availability alone can explain much of the reduction in reproductive success in insectivorous woodland bird species occupying temperate urban environments. Other known urban stressors, such as various types of pollution, human disturbance, and perceived predation risk, could have also influenced the nestlings. However, they appear to play only a limited direct role in lowering the productivity of insectivorous passerines in these situations. Furthermore, the indirect effects of certain stressors (e.g. habitat modification, light pollution) on birds via reducing urban populations of moths and other insects might be still substantial.

The positive effects of supplementary food on urban nestlings' body size and survival were clearly detectable and strong compared to previous studies in urban great tit populations (Bańbura *et al.* 2011, Demeyrier *et al.* 2017). Although these earlier studies differ in several methodological details from our experiment (measured traits, length of food supplementation, type of food, etc.) the much stronger effect we found may arise primarily due to the enhanced quality of mealworms and the higher amounts of extra food per nestling we provided throughout most of the brood-rearing period. Alternatively or additionally, the natural availability of arthropods may be lower in our urban site than in the habitats involved in the above studies, making supplementary food more valuable and effective in our experiment (Ruffino *et al.* 2014).

The estimated biomass of arboreal caterpillars (the optimal nestling food for many passerines; Cholewa & Wesołowski, 2012) during the brood-rearing period in our urban site was extremely low (approximately 8-times higher in the forest site; and similar even more dramatic differences in caterpillar biomass occur in other years (2013-2016, Figure S.IV.1; Seress *et al.* 2018), but we consider such differences to be a common feature of urban environments (Shawkey *et al.* 2004, Marciniak *et al.* 2007, Pollock *et al.* 2017, Hajdasz *et al.* 2019).

The strong treatment effect that we found on urban but not forest birds' breeding success is unlikely to be driven by the more extensive use of supplementary food by urban parents than those in the forest habitat for three reasons. First, the amounts of leftover food was very low in both habitats, and consecutive nest checks on day 15 (i.e. food supplementation and later that day, nestling measurements) also indicated that birds usually consumed all the provided food within a few hours. Second, the video recordings confirmed that the supplemented mealworms were utilized predominantly by supplemented parents in both habitats. Finally, the videos confirmed that the proportion of mealworms in the nestling diet was high in both urban (81%) and forest (75%) supplemented broods. It thus appears clear that forest birds are not food limited, and importantly that supplementary feeding with nutritionally enhanced mealworms provided forest supplemented pairs with a food source that was of broadly similar nutritional quality to the food sources utilised by forest control pairs – otherwise one would expect supplemented pairs to have lower nestling body size and survival rates than the controls.

Besides the presumable direct (calorific and nutritional) benefits of the extra arthropod food on urban broods, indirect mechanisms might also have played a role in improving brood performance. For example, supplementary food may have indirectly helped urban nestlings by mitigating the effects of various stressors (e.g. parasites, heat stress) in the urban environment. Furthermore, the parents of supplemented broods consumed significant proportions of the mealworms themselves, and this tended to be higher in urban pairs. The resultant reduction in the time parents needed to invest in foraging for themselves, and the potentially higher body condition, may have enabled females to invest more in brooding and feeding young nestlings. Additionally, food supplementation can also enhance breeding success by increasing parents' nest defence behaviour, for example because parents can spend more time in the proximity of their nest and thus defend it against predators (see Vafidis *et al.*, 2018 and references). We did not record brood losses attributable to nest predation in any of our experimental groups, thus it is unlikely that this latter mechanism played an important role in our case – although it may be important in other regions or species with higher rates of nest predation.

Finally, our data can provide a broad indication of the magnitude of urban food limitation in this study system. Supplying 40-50% of urban nestlings' food requirements enabled them to more or less match the performance of forest broods. This implies that, at current densities and brood sizes, urban caterpillar populations need to be doubled if urban and rural chicks are to have similar performance without supplementary food. Urban great tit brood sizes are, however, typically c. 75% of those of forest broods in our study areas (Seress *et al.* 2018). Assuming that such reductions are driven by food limitation and that clutch size linearly increases with food availability it seems likely that urban caterpillar populations need to be increased by at least a factor of 2.5 to equalise urban and forest great tit brood size and performance. However, much higher increases are likely to be required given that other urban passerine species, including other tit species or woodpeckers (Smith & Smith 2019), also depend on caterpillars for provisioning their young and will thus compete to some extent with great tits. Achieving such large increases will be challenging – although there is substantial capacity to increase the volume of urban tree canopy through tree planting (Kroeger *et al.* 2018), the benefits of this would take time to accumulate and many urban trees fail to come close to their mature size due to high mortality rates (Widney *et al.* 2016). Furthermore, it would also be crucial to significantly shift the urban plant composition towards native species, as these are known to support more abundant and diverse insect communities compared to exotic non-native species (Narango *et al.* 2018, Tallamy *et al.* 2020).

This study provides rare experimental evidence for the strong effects of food limitation on urban nestling size and survival rates. Provision of mealworms that are fed on an enriched diet removed or considerably reduced the marked differences in nestling size and survival rates between non-supplemented urban and forest broods. Our focal species specialises on provisioning nestlings with caterpillars, which is a common strategy in many groups of birds occurring in urban areas across the temperate zone including tits, chickadees, finches, and woodpeckers. Thus, food limitation may be a similarly major factor limiting reproductive success in several other urbanized bird species. The provision of higher quality supplementary food to such species during the breeding season may increase the body size and nestling survival rates in their urban populations. The increased growth might have also yielded additional fitness advantages for urban supplemented broods given that effects of early nutritional conditions can be carried to adulthood, affecting adult body size (e.g. Cleasby *et al.*, 2011) or even cognitive abilities such as song learning (S. *et al.* 2002). Urban nestlings' benefit from the arthropod-rich food was especially prominent in their pre-fledging body mass (ca. 2 grams), which might have also increased their recruitment rate (Schwagmeyer & Mock 2008) given that pre-fledging body

mass correlates positively with post-fledging survival in many passerine species, including great tits (Magrath 1991). To what extent could the increased nestling survival and development contribute to urban populations' size and stability, is still an unanswered question though. For example, whilst supplementary feeding improved breeding success in sub-urban house sparrows (Peach *et al.* 2014) this did not generate an increase in population size (Peach *et al.* 2018). Whilst further work on the impacts of supplementary feeding on population dynamics is certainly needed, it is clear that the decreased abundance of key arthropod food sources in urban areas can limit avian reproductive success. Thus, management methods that overcome this limitation are likely to be beneficial in supporting and enhancing urban biodiversity, especially considering the marked and ongoing decline of global insect populations (see Owens *et al.* 2020 and references in it).

CHAPTER V.

DIFFERENCES IN FEATHER STRUCTURE BETWEEN URBAN AND FOREST GREAT TITS: CONSTRAINT OR ADAPTATION?

Abstract

Urbanization is one of the strongest habitat transforming processes today that has resulted in changes in the ecological conditions for wild populations. In birds, the limitation of natural food sources and a warmer microclimate in cities can potentially influence the development and functioning of the plumage that may have important fitness consequences. Despite its potential significance, the plumage structure of urban birds are largely unexplored and it is unclear whether and how they respond to urban ecological processes such as different constraints and selection pressures. In this study, we compared several structural properties of contour, wing primary and tail feathers between two forest and two urban great tit *(Parus major)* populations. Our results show that the urban environment affects only a few structural properties of feathers and only in the plumage of first-year birds. We found that both the plumulaceous and the pennaceous parts of their contour feathers were longer and had lower barb density in the urban than in the forest habitat. We also found that the primaries of first-year birds had narrower rachis and higher barbule density in the cities than in the forests, but there were no differences in other wing feather traits and in any tail feather traits between habitats. We did not find differences in the feather structure of urban versus forest adult birds. The habitat differences in first-year birds may indicate nutritional constraints or the effects of the warmer microclimate of the urban environment. These differences seem to disappear completely by adulthood that can be explained by the selective mortality of first-year birds, or by adults being less sensitive than first-year birds to environmental effects during their moult.

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5.1. Introduction

Passerine birds in temperate geographic regions renew their worn plumage at least once annually during moulting (Jenni & Winkler 2020). Growing feathers is an energy and nutrient-demanding process (Lindström *et al.* 1993), and the quality of the new feathers is strongly affected by the individuals' physiological state and hence by the prevailing environmental conditions during this period (e.g. Swaddle & Witter 1997, DesRochers *et al.* 2009). In addition, adaptive changes in response to different environmental conditions can generate structural differences in feathers (e.g. in the densities of contour feathers) even within populations (Koskenpato *et al.* 2016).

Urbanization is amongst the most severe anthropogenic habitat transformation processes that pose significant impacts on animal populations (Seress & Liker 2015, Fenoglio *et al.* 2020). Even though birds are amongst the most studied taxa in urban ecology, so far very few studies have explored how urban environments influence one of their most important characteristics, the feathers (except for plumage coloration; see ***Chapter I,*** section *1.3. Plumage - how can be affected by urban habitats?*). A study of Mountain chickadees *(Poecile gambeli)* showed that feather growth rate was significantly faster in urban compared to forest nestlings, which presumably resulted in poorer feather quality in urban individuals (Marini *et al.* 2017). Furthermore, as the relationship between feather growth rate and feather quality is condition-dependent (Vágási *et al.* 2012), urban birds may suffer additional disadvantages in plumage quality if they have poorer body condition (e.g. in yearling: Jiménez-Peñuela *et al*. 2018 and male house sparrows *Passer domesticus:* Dulisz *et al.* 2016; but also see Bókony *et al.* 2012, Meillère *et al.* 2015).

One of the major changes birds have to face in urban environments is the drastically altered quantity and quality of food sources (e.g. fewer invertebrates but abundant anthropogenic food; Jones & Leather 2012, Seress *et al.* 2018, Nadolski *et al.* 2021, see ***Chapter I,*** section *1.1. Food limitation in urban habitats*) that is known to affect several key life-history characteristics, including reproductive success (Peach *et al.* 2015, Pollock *et al.* 2017, Seress *et al.* 2020), body size (Heiss *et al.* 2009, Meyrier *et al.* 2017). The quality and quantity of available food strongly affect the structural properties of the wing and contour feathers during the moulting period (Murphy and King 1992, Pap *et al.* 2008, Broggi *et al.* 2011, Jenni and Winkler 2020, but see Pap et al. 2015) and very probably also during the nestling stage when the first feathers are being grown (Sillanpää *et al.* 2010). Inadequate nutrition can result in shorter and weaker (more flexible) feathers and changes in the density of the feathers' vane (Pap *et al.* 2008, Broggi *et al.*

2011). These changes may ultimately affect the flight performance of birds and the insulating properties of their plumage (Muller & Patone 1998, Heers *et al.* 2011).

Another prominent feature of urban landscapes is the significantly drier and warmer microclimate, known as the urban heat island effect (UHI; Oke 1982, Cui & Shi 2012; see ***Chapter I,*** section *1.2. Urban heat island*). This results in a higher risk of heat stress (Ward *et al.* 2016) that can affect nestling development (Pipoly *et al.* 2013) and increase mortality (McKechnie & Wolf 2010). Although rapid adaptive changes in response to the UHI were described in urban populations (see ***Chapter I,*** section *1.2. Urban heat island*), but such studies in birds remained very rare (Pipoly *et al.* 2022). Changes in environmental temperature may affect the structural properties of the plumage (e.g. through phenotypic plasticity or genetic adaptation), especially in contour feathers, however, earlier studies reported conflicting effects. For example, Koskenpato *et al.* (2016) found significantly denser insulating parts (e.g. plumulaceous part) of the dorsal contour feathers in cold-tolerant morphs of tawny owls *(Strix aluco),* suggesting that contour feathers with denser insulating parts are adaptive in colder environments. However, in a multispecies comparative study, Pap *et al.* (2017) found a seemingly opposite pattern, i.e. that the feathers of bird species wintering in colder areas are less dense. Their explanation for this latter result was that less dense plumage can be capable of trapping higher amounts of air near the body surface, thus enhancing the insulation capacity of the plumage. Similarly, the comparisons of feather structure of birds living at different altitudes produced inconsistent results. First, Cheek *et al.* (2018) did not find differences in the structural properties of contour feathers between high and low-altitude populations of torrent ducks (*Merganetta armata*). In contrast, in a comparative study, *Barve et al.* (2021) showed that the contour feathers of passerine species living in high (hence colder) altitudes have a higher proportion of plumulaceous section that they interpreted as a possible adaptation for more efficient insulation. The heterogeneity of these results may either reflect different responses to environmental factors within or between species, or differences in the climatic characteristics of the studied environments. Thus, these conflicting conclusions of the earlier studies make it difficult to predict how environmental temperature influences feather properties in a particular species. It is important to note here, however, that none of the above-cited studies examined plumage density which is also an important factor in heat dissipation (Jiang *et al.* 2010). In fact, several studies suggest that looser plumage allows for better heat dissipation, thus facilitating heat tolerance (e.g. Deeb & Cahaner 1999, Jiang *et al.* 2010, Nord & Nilsson 2019). For example, experimental studies on poultry showed that broilers with fewer feathers (e.g. naked neck breeds) can develop better (Deeb & Cahaner 1999) and have higher survival chances (Jiang *et al.* 2010)

under warm conditions than broilers with higher feather densities. Nord & Nilsson (2019) observed a similar pattern in wild birds: feather-clipped blue tits (*Cyanistes caeruleus*) were less limited by heat dissipation during the nestling rearing period, which led to a better foraging efficiency and the production of larger and heavier nestlings.

In this study, we aim to explore how urbanization affects the structural properties of feathers of great tits (*Parus major)*, a small insectivorous passerine that is non-migratory in our study region. To do so, we compare several traits of the contour, wing, and tail feathers between urban and forest populations. We expect that – similarly to many other traits – plumage characteristics should differ between urban and non-urban populations, due to one or more of the reasons detailed above. Predicting the effects of urbanization on the structural properties of feathers is difficult, however, because the few earlier, mostly correlative studies produced conflicting results (see above). On the one hand, we expect that between-habitat differences in some of the structural properties of feathers may yield lower quality feathers in urban than forest individuals, for example, due to environmental constraints like food limitation during feather development (nestling stage or moulting of adults). Thus, we predict shorter and weaker (more flexible) flight feathers with altered vane densities (Murphy *et al.* 1988, Pap *et al.* 2008, Meillère *et al.* 2017), and contour feathers with shorter and denser feather vanes (Butler *et al.* 2008, Broggi *et al.* 2011) in urban than in forest birds. On the other hand, we can also anticipate adaptive changes in urban birds' feather structure. For example, due to their smaller body size (Barve *et al.* 2021) or changes in flight distances (e.g. due to larger foraging areas; Jarrett et al. 2020), we can expect changes in adult birds' flight feathers. Furthermore, adaptive changes in contour feather traits may help urban birds to better cope with the effects of UHI. In the latter case, we expect less dense feather structure in urban birds allowing for better heat dissipation (Koskenpato *et al.* 2016, Nord & Nilsson 2019 but see Pap *et al.* 2017, Barve *et al.* 2021). Because the environmental effects can affect first-year birds (henceforth "FY"; birds that underwent only one partial post-juvenile moult) stronger than adults (henceforth after first year birds, "AFY"; birds that underwent at least one complete post-breeding moult), we analysed these age groups separately. To our knowledge, this is one of the first studies that comprehensively tests differences in feather structural properties between urban and forest populations.

5.2. Methods

5.2.1. Feather sample collection

We carried out our study between November 2016 and July 2018 in two urban and two forest populations of great tits in Hungary (for more details see ***Chapter III***). We captured great tits during two consecutive breeding seasons (April-June, in 2017 and 2018) by using nestbox traps (n = 160 birds), and two consecutive winters (November-February, in 2016/2017 and 2017/2018) with mist nets close to the middle point of our study sites (n = 51 birds). We sampled all individuals only once during the study period and performed a similar number of bird catches throughout the study period in each study area. Upon capture, we plucked 3-5 yellow contour feathers from the upper side of the breast (Figure V.1a) and also collected the innermost primary (P10) from the right wing and the second outermost tail feather (R5) from the left side from each individual. Feather samples were stored in dry paper envelopes until the subsequent analyses.

Captured birds were ringed with numbered metal rings (if ringless), and we also determined their sex (n = 113 female, n = 98 male) and age (n = 127 first-year birds, henceforth "FY"; n = 84 birds after the first year, henceforth "AFY") based on their plumage characteristics (Svensson 1992). We differentiated between two age groups, FY and AFY because these birds grew their feathers under different developmental conditions (detailed below), which may ultimately affect their feather quality. For example, the feather quality of FY birds depends on the conditions experienced both during the nestling development stage (when it may be in trade-off with other developmental processes) and the post-juvenile moulting (when juveniles are less experienced in foraging than older birds). In our dataset, the FY birds underwent only one, so-called partial post-juvenile moult, typically a few weeks after fledging. The post-juvenile moult includes some or all of the tail feathers and tertials, and all of the contour feathers, but does not include the primaries, secondaries, or primary coverts (Jenni & Winkler 1994, 2020). Thus, wing feathers collected from FY birds were grown during the nestling stage, while their body and tail feathers were replaced during their post-juvenile moult. AFY birds were any other birds that underwent at least one complete post-breeding moult, i.e. they have already renewed their entire plumage at least once (Svensson 1992). As moulting conditions (e.g. food quantity and quality) may significantly vary between years, we also used these age categories to determine the calendar year when the collected feather had been grown for each individual (note that this is not necessarily the same as the year of sampling, e.g. for birds captured in January). Finally, in our study region, partial migration during winters may occur in some great tits populations (Török 2009). Therefore, and very importantly, during the winter sampling, we collected feathers only

from recaptured individuals that were either registered as breeders or fledglings at the site of capture – this way we ensured that these birds indeed replaced their feathers on the same study site where they were feather sampled during the winter. Note that according to our ringing data habitat switching (i.e. movements between our urban and forest study sites) seems to be extremely rare (our unpublished data), and we excluded all such birds from the current study.

5.2.2. Feather measurements

For all feather types, we took measurements only on intact feathers (which were clearly not broken to avoid any bias in feather length measurements; this was the case in only a very few birds in total) and feather sections (e.g. avoided parts where barbs or barbules were missing to avoid biases in density measurements). In the case of the contour feathers, we measured three feathers from each individual and used the average values of these measurements in the statistical analyses. First, we took stereomicroscopic photos of each contour feather on a millimeter grid background. Then, we determined the borderline between the proximal plumulaceous and the distal pennaceous parts of the feather along the rachis. The division between the two parts were at the base of the barb on which the proportion of plumulaceous barbules was at least 33% of the total barbules (Pap *et al.*, 2017, Figure V.1a). Finally, we determined the scale of each photo by using the millimeter grid background, and measured: (1) length of the plumulaceous and the (2) pennaceous parts (always measured between the pennaceous–plumulaceous regions' borderline and the base of the last barbs), as well as the total number of (3) plumulaceous and (4) pennaceous barbs. Then we divided the number of barbs by the corresponding rachis length to determine the density (barbs/mm) of the two parts of the feather (henceforth (5) 'plumulaceous barb density' and (6) 'pennaceous barb density'). Note that the length of the pennaceous part can be significantly affected by feather abrasion. Thus to avoid any potential bias resulting from abrasion, (i) we measured the pennaceous section's length until the base of the last barbs (i.e. until the last branching on the distal part of the feather; Figure IV.1a, green line), and (ii) involved only clearly intact contour feathers to our measurements.

For each P10 (wing) and R5 (tail) feather, we determined (1) length, (2) rachis width (diameter), (3) barb density, and (4) barbule density. Feather length was measured with a ruler along the rachis to the nearest 0.5 mm and rachis width was measured with a digital caliper to the nearest 0.01 mm at the base of the vane (i.e. at the base of the most proximal barbs). For the vane density measurements, we first took digital photographs using a stereomicroscope (Nikon SMZ800) with a camera (Moticam 10). The pictures were centered on the middle point of the

inner feather vane, using a millimeter grid background for size reference. Then, we analyzed these images using ImageJ software (v. 1.51; https://imagej.nih.gov/ij/). Using the metric grid background, we determined the exact scale for each photo and determined barb density as the number of barbs along a 1 cm long section designated parallel to the rachis (Figure V.1b), and barbule density as the number of barbules along a 1 mm long section of a barb (Figure V.1c), respectively. KS performed all of the measurements on feathers, and all variables showed high within-observer repeatability (for more details see Table S.V.6).

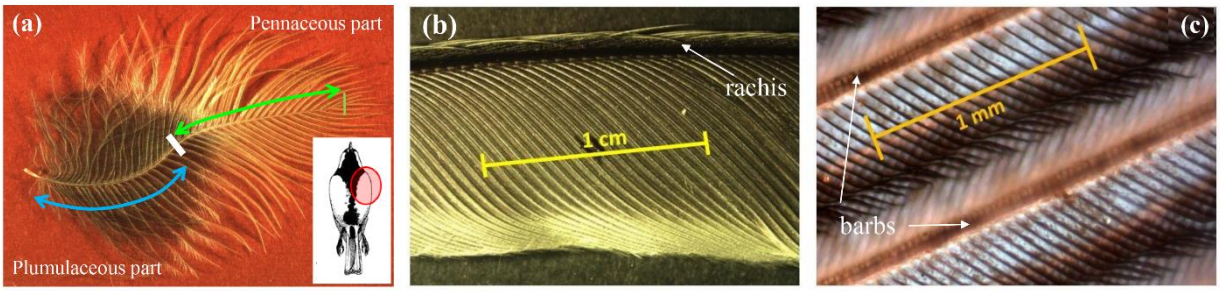


Figure V.1. Figure (a) shows the borderline (white line) between the plumulaceous (blue arrow) and the pennaceous (green arrow) part of the contour feathers. Contour feathers were collected from the upper side of the breast (as shown in the inset). Note that we measured the length of the pennaceous section until the base of the last barbs (i.e. until the last branching; small green line), and only involved intact feathers, to avoid any potential bias resulting from feather tip abrasion on these measurements. On the wing and tail feathers, the number of (b) barbs and (c) barbules was measured on a 1 cm and 1 mm long section, respectively, at the middle point of the vanes.

5.2.3. Statistical analysis

To test the effects of the habitat type (i.e. urban versus forest) on feather structure we conducted pre-planned comparisons between the two habitat groups (i.e. differences between the two urban and the two forest sites) following the approach suggested by Ruxton & Beauchamp (2008), which consisted of two steps. First, we fitted linear models (LM) separately for each measured feather trait (as dependent variable). These models included the study site (four levels), sex, age (FY or AFY), year of moult (2016 or 2017 as factor) as predictors, and the site × age interaction. Note that fitting these models is a necessary first step for the main analysis of the study, the calculation of linear contrasts, and we did not base the conclusions of our study on these models.

In the second step, we used these linear models for each response variable to conduct the pre-planned comparisons (regardless of the results of the first stage analysis) by calculating linear contrasts (package *'emmeans'*) between the two forest and two urban sites (for similar approach see also Pipoly *et al.* 2019, Vincze *et al.* 2019) separately for FY and AFY birds. We compared habitats separately for the two age groups because they likely differed in their moulting

conditions (see above the section '*Feather sample collection'*). Since our main predictor (study site) has only four levels, this approach of using pre-planned comparisons is more appropriate than including the study site as a random factor that would result in unreliable estimations (Piepho *et al.* 2003). Furthermore, including both habitat and study site as fixed effects in the models is also not feasible because of the high collinearity between these predictors (Piepho *et al.* 2003, Dormann *et al.* 2013). Our pre-planned comparison is similar to an experiment with two control and two treatment groups, where we test the differences between the two control (i.e. forest) and two treatment (i.e. urban) groups. Note that a significant site effect (or site × age interaction) detected in the linear model does not necessarily reflect a significant habitat effect (or different habitat effects in the age groups) in the linear contrast analyses because these effects may be inconsistent between the sites within the same habitat type. Conversely, even a weak site effect may produce a detectable difference in the habitat comparisons.

Since feather abrasion can potentially affect feather length (see above) we ran preliminary analyses to test whether birds sampled in winter and summer, respectively, differed in their feather lengths due to the potential effects of abrasion. For wing and tail feathers, the effect of the capture season was non-significant ($p > 0.1$ in all models), and including 'season' to the feather length models did not change the conclusions of habitat comparisons. Although we found a significant season effect for the pennaceous length of the contour feathers, this did not change the conclusion of habitat comparison assessed by linear contrasts (Table S.V.5). Therefore, in the further steps, we used the model without the season variable.

5.3. Results

5.3.1. Contour feathers

We found differences between habitats in the characteristics of contour feathers, although the habitat effects differed between the two age groups. We found a significant site × age interaction for the pennaceous (distal), but not for the plumulaceous (proximal) barb density (see Table S.V.1 for the results of a linear model that contains site and age effects and their interaction). The linear contrasts showed that both pennaceous and plumulaceous parts of the contour feather were significantly less dense in FY urban than in FY forest birds, whereas no barb density difference was detected in AFY birds (Table V.1, Fig. V.2a, b). Next, to explore if changes in the length or number of barbs drive the observed differences in density, we performed similar analyses in the case of these two variables. The linear contrasts calculated between the urban and forest birds (i.e. between the two urban and two forest sites, using the estimates of the linear model) indicated

that both the pennaceous and plumulaceous parts were significantly longer in urban FY than forest FY birds, while there was no such difference in AFY birds (Table V.1, Fig. V.2c, d). Finally, in the case of the number of barbs, the linear contrasts did not show any consistent habitat difference in either of the two feather sections in either age group (Table V.1).

Table V.1. Differences in the structural properties of the contour feathers between urban and forest great tits (*mean* ± *SE* and sample size) were tested separately for first-year (FY) and after first year (AFY) birds. Statistically significant ($p < 0.05$) differences based on the linear contrast analyses are highlighted in bold (see Table S.V.3 for details of the linear contrasts).

	Contour feathers	
	Forest	Urban
Pennaceous density (barbs/mm)		
FY	**2.43 ± 0.03 (62)**	**2.34 ± 0.03 (64)**
AFY	2.41 ± 0.04 (50)	2.45 ± 0.06 (32)
Plumulaceous density (barbs/mm)		
FY	**3.44 ± 0.03 (62)**	**3.34 ± 0.03 (64)**
AFY	3.54 ± 0.04 (49)	3.51 ± 0.05 (32)
Pennaceous length (mm)		
FY	**7.45 ± 0.14 (62)**	**7.83 ± 0.11 (64)**
AFY	8.02 ± 0.16 (50)	7.58 ± 0.18 (32)
Plumulaceous length (mm)		
FY	**8.58 ± 0.14 (62)**	**9.11 ± 0.17 (64)**
AFY	8.48 ± 0.14 (50)	8.88 ± 0.18 (32)
Total number of pennaceous barbs		
FY	17.88 ± 2.00 (62)	18.22 ± 2.03 (64)
AFY	18.97 ± 2.34 (50)	18.34 ± 1.65 (32)
Total number of plumulaceous barbs		
FY	29.34 ± 2.55 (62)	37.18 ±2.92 (64)
AFY	29.85 ± 2.22 (49)	30.97 ± 2.08 (32)

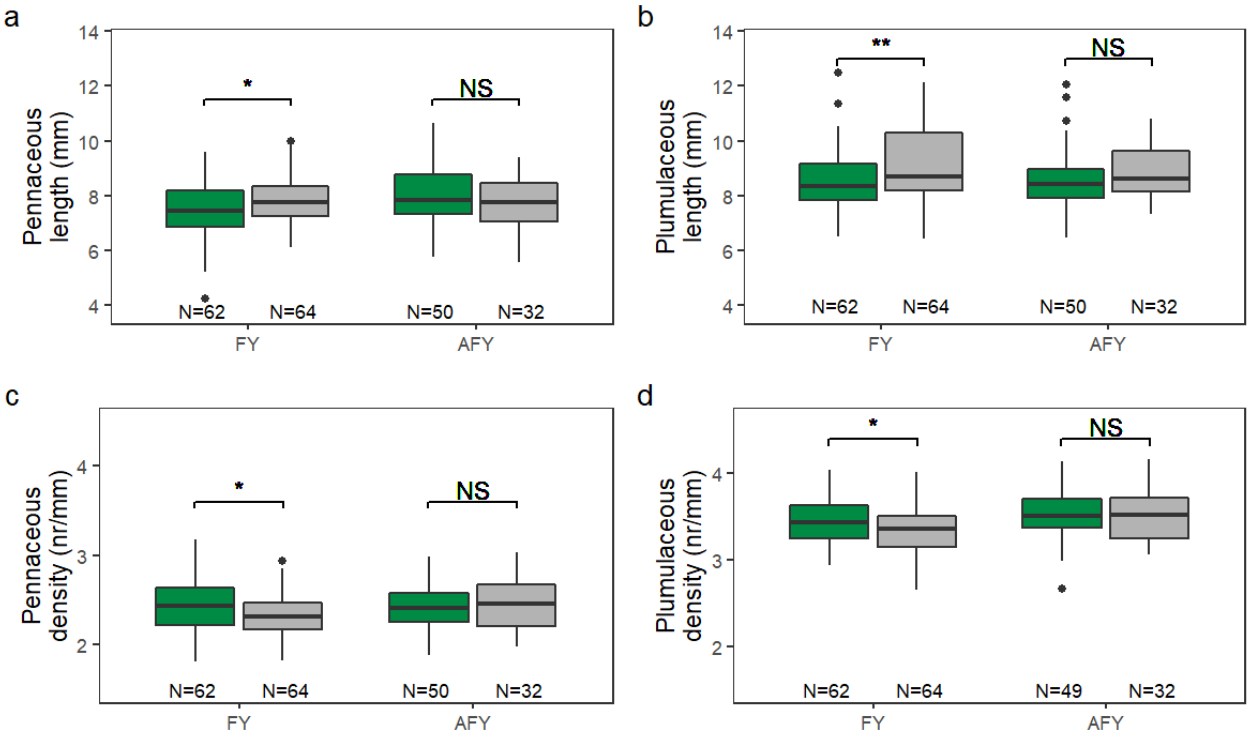


Figure V.2. Differences (a, b) in the length and (c, d) in the density of the distal pennaceous (a,c) and proximal plumulaceous (b, d) part of contour feathers between forest (green) and urban (grey) first-year (FY) and after first year (AFY) great tits. * and ** indicate statistically significant habitat differences at $p < 0.05$ and $p < 0.01$ levels, respectively (see Table S.V.1 and Table S.V.3 for details of the statistical comparisons). Medians, interquartile ranges and data ranges are shown by the middle thick lines, the boxes, and the whiskers, respectively.

5.3.2. Wing and tail feathers

Urban and forest birds also differed in some of their wing feather traits (Fig. V.3). Specifically, linear contrasts showed a significant habitat difference in the FY but not in AFY birds (Table V.2a): the wing feathers of urban FY birds had significantly narrower rachis (Fig. V.3b) and significantly higher barbule density (Fig. V.3d). Furthermore, the habitat contrasts did not indicate consistent differences in rachis width between urban and forest birds in either age group (Table V.2). We did not find any significant habitat difference in other variables for either wing or tail feathers (Table V.2).

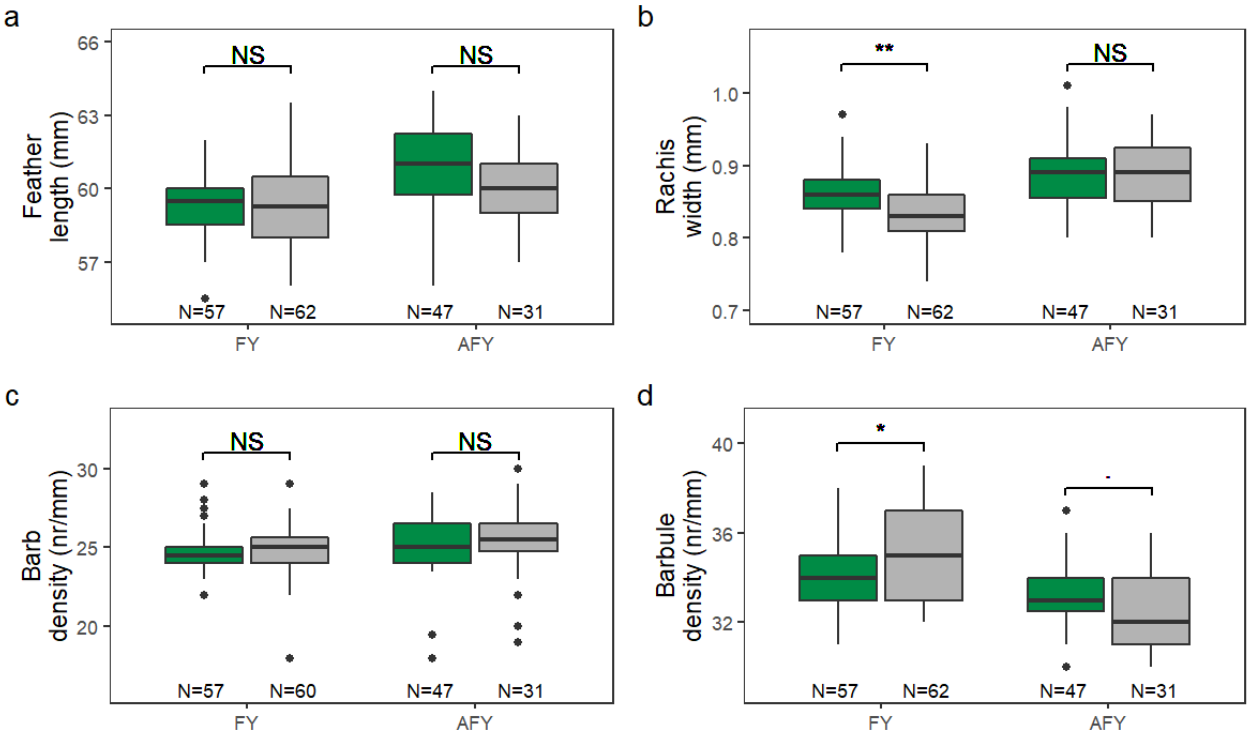


Figure V.3. Differences in (a) feather length, (b) rachis width, (c) barb- and (d) barbule density of the wing feathers (innermost primary) between forest (green) and urban (grey) first-year (FY) and after first year (AFY) great tits. * and ** indicate statistically significant habitat differences at $p < 0.05$ and $p < 0.01$ levels, respectively (see Table S.V.2 and Table S.V.4 for sample sizes and details of the statistical comparisons). Medians, interquartile ranges and data ranges are shown by the middle thick lines, the boxes, and the whiskers, respectively.

Table V.2. Differences (*mean* ± *SE* and sample size) between urban and forest first-year (FY) and after first year (AFY) great tits in the structure of (a) wing and (b) tail feathers. Statistically significant ($p < 0.05$) differences based on the linear contrast analyses are highlighted in bold (see Table S.V.4 for details of the linear contrasts).

	(a) Wing feathers		(b) Tail feathers	
	Forest	Urban	Forest	Urban
Feather length (mm)				
FY	59.33 ± 0.18 (57)	59.25 ± 0.22 (62)	66.27 ± 0.30 (52)	66.11 ± 0.36 (58)
AFY	60.72 ± 0.29 (47)	60.11 ± 0.31 (31)	67.74 ± 0.35 (45)	67.45 ± 0.33 (28)
Rachis width (mm)				
FY	**0.86 ± 0.00 (57)**	**0.84 ± 0.01 (62)**	0.79 ± 0.01 (55)	0.79 ± 0.01 (59)
AFY	0.88 ± 0.01 (47)	0.89 ± 0.01 (31)	0.79 ± 0.01 (45)	0.80 ± 0.01 (28)
Barb density (nr. of barbs/1 cm)				
FY	24.59 ± 0.18 (57)	24.80 ± 0.20 (60)	17.48 ± 0.17 (55)	17.41 ± 0.19 (59)
AFY	25.15 ± 0.33 (47)	25.39 ± 0.41 (31)	17.28 ± 0.18 (44)	17.83 ± 0.24 (27)
Barbule density (nr. of barbules/1 mm)				
FY	**33.98 ± 0.19 (57)**	**34.98 ± 0.26 (62)**	31.16 ± 0.24 (55)	31.86 ± 0.26 (59)
AFY	33.32 ± 0.23 (47)	32.55 ± 0.34 (31)	31.60 ± 0.35 (45)	31.07 ± 0.37 (28)

5.4. Discussion

5.4.1. Contour feathers

Our results show that the properties of contour feathers significantly differed between urban and forest habitats in FY, but not in AFY birds. Specifically, the contour feathers of urban FY birds had significantly less dense pennaceous and plumulaceous sections compared to forest FY birds. Importantly, this decrease in density was driven by the elongation of these feather sections and not by the decrease in the number of barbs in these feathers.

Some of these differences in FY birds' contour feathers may reflect the limited food availability in cities during the moulting period. A few weeks after fledging FY great tits undergo the partial post-juvenile moult, during which they replace all of their contour feathers (Jenni and Winkler 2020; ***Chapter V,*** section *5.2. Methods*). At this time, FY birds are still relatively inexperienced (Heise & Moore 2003) and may have especially low foraging efficiency in food limited environments like cities (Nadolski *et al.* 2021; including our urban study sites, see Seress *et al.* 2018, 2020). Later, by the time of their first post-breeding moult as AFY birds, individuals become more experienced in foraging (Heise & Moore 2003), which can help them to develop higher-quality plumage – similar to that of the forest birds –, therefore the differences present in FY birds' contour feathers may disappear in later life phases. This food limitation explanation, however, is seemingly contradicted by our findings that contour feathers were actually longer in urban than in forest FY birds, which also explains urban birds' lower barb densities. Developing longer feathers may require more nutrients, thus this result does not indicate food shortage. This latter interpretation is in line with the results of other studies. For example, the study of Butler *et al.* (2008) found shorter contour feathers in nestlings *versus* adult passerines (interpreted as a result of trade-offs during nestlings' ontogeny), while Broggi *et al.* (2011) reported shorter and denser contour feathers in adult great tits in northern *versus* southern populations (explained by energy and time constraints in the former population). Alternatively, it is also possible that birds allocate the same amount of nutrients to feathers of different lengths, for example by growing longer feathers that have thinner rachis or fewer barbs and/or barbules. However, the lack of habitat difference in the number of barbs of contour feathers did not support this idea but the testing of this mechanism requires further investigations with more detailed and sensitive measurements (e.g. counting the number of barbules or measuring the mass of these feathers). A second explanation is that urban FY birds' contour feathers reflect an adaptation to the warmer climate in cities. For example, Koskenpato *et al.* (2016) found that a denser contour feather

structure serves better insulation and other studies also showed that plumage density (measured as the number of feathers per body surface area) correlates negatively with ambient temperatures (Deeb & Cahaner 1999, Møller 2015, Osváth *et al.* 2018). These latter results also imply that less dense plumage (achieved either *via* less dense feather structure or lower plumage density) may promote better heat dissipation in warmer conditions (Nord & Nilsson 2019) and may also reduce the heat conduction through the solid elements of the feathers (Wolf & Walsberg 2000). Therefore, the looser feather structure we observed in our urban FY birds may indicate an increased capacity of heat dissipation – an explanation that is also consistent with the fewer body feathers and larger bare body surfaces we found in the same study system in urban *versus* forest great tit nestlings (Sándor *et al.* 2021). Note that although such changes in plumage characteristics may aid urban birds to cope with increased temperatures, other physiological processes of cooling are probably also very important to maintain optimal body temperature. Furthermore, the relationship between temperature and the structure of contour feathers is not straightforward by the results of other studies. For example, unlike Koskenpato *et al.* (2016), other studies suggest that long and less dense feathers (especially on the plumulaceous section) provide better insulation by trapping increased volumes of air (Butler *et al.* 2008, de Zwaan *et al.* 2017, Pap *et al.* 2017, Barve *et al.* 2021). Further experimental studies are required to corroborate whether the looser feather structure we found in urban birds really helps their heat dissipation.

Finally, the exact timing of breeding also differs slightly between urban and forest populations (urban birds start breeding on average 6-7 days earlier than forest ones in our study sites, for more details see "Breeding phenology and breeding success of Great Tits" section in Seress *et al.* 2018; and see also Marini *et al.* 2017, Sepp *et al.* 2018). This may affect the amount of time available for moult (Hope *et al.* 2016) that can ultimately affect the quality of the plumage (e.g. Dawson *et al.* 2000, de la Hera *et al.* 2009, but see Echeverry-Galvis & Hau 2013). Thus, the longer body feathers in urban FY birds might be the result of the longer time available for moulting, enabling slower feather growth in these habitats (Vágási *et al.* 2012). However, this explanation also predicts a similar difference in adults, which is not supported by our results.

5.4.2. Flight feathers

The flight feathers of urban and forest great tits were similar in most respects. In the FY age group, however, we found significantly narrower rachises and higher barbule densities in the wing feathers of urban compared to forest birds – a difference that was not present in older birds.

The wing feathers of FY birds were grown during the nestling phase, and develop at the fastest rate exactly when nestlings are in the process of the fastest growth (at 5-10 days of age, Orell 1983). Therefore, the quality of these feathers may be in trade-off with the ontogenetic development of other traits. It is quite likely that limited food availability affects not only nestlings' body size but also the quality of their flight feathers. Our results that urban compared to forest FY birds have narrower rachises and higher barbule density in their wing feathers are partly in line with our predictions, and also with the results of several previous experimental studies. These earlier works showed that certain negative factors (Dawson *et al.* 2000, Pap *et al.* 2008, 2013, Vágási *et al.* 2012), as well as increased feather growth rates (Marini *et al.* 2017), can result in narrower rachis in flight feathers (Dawson *et al.* 2000). Such structural change suggests lower quality (Vágási *et al.* 2011) and more flexible feathers, that are less resistant against high aerodynamic forces during the flight (De La Hera *et al.* 2010).

The higher barbule density we observed in the wing feathers of urban FY birds may contradict our initial predictions and the results of some previous studies (DesRochers *et al.* 2009, but see Pap *et al*. 2013) if it is the consequence of an increase in the total number of barbules. On the other hand, it may also be the result of the shortening of the barbs without any changes in the number of barbules. Unfortunately, our microscopic photos were not suitable for the accurate measuring of the length of barbs, thus we cannot decide which process resulted in higher barbule density in the urban birds. These structural characteristics of FY birds' wing feathers may result in increased mortality (Minias *et al.* 2015, Szép *et al.* 2019), offering a plausible explanation for the lack of habitat differences between AFY birds in our study.

Finally, we didn't find any habitat differences in tail feathers' structural properties in either age group. The lack of any habitat difference suggests that FY birds may invest more in the quality of their tail feathers during the post-juvenile moult to maintain the role of these feathers in flight and manoeuvring. So far the only study comparing tail feathers' structural properties between urban and non-urban birds documented less dense feather structure (measured as the feather mass/length ratio) in urban than non-urban juvenile house sparrows and found no habitat difference in adults (Meillère *et al.* 2017). This, along with our results, implies that the urban environment affects birds' plumage differently at different life stages.

5.4.3. Conclusions

Overall, on a robust sample size and by involving two replicates per habitat type, we found urban *versus* forest differences only in a few structural properties of feathers, and these were present only in FY birds. Based on our results, both constraints due to food limitation and adaptive responses to urban microclimate may play a role in shaping urban birds' feather structure. Interestingly, we found no differences between habitats in the feather structure of AFY birds, which can be explained either by selective mortality of FY birds or lower sensitivity to environmental stress in AFY birds. As this is a correlative study, we cannot firmly differentiate between these explanations. It also remains an open question how significant the observed habitat differences are for the key functioning of the plumage. Experiments would be needed to better understand how certain factors change the structure, and ultimately the function of urban birds' feathers (for more details see ***Chapter VII.***). To fill up this knowledge gap, we suggest that future experimental studies are needed to better understand 1) what factors affect the quality of feathers in cities and how, 2) whether feather structure properties observed in urban young birds affect their condition and survival, and 3) how the habitat differences observed in contour feathers could play a role in the heat dissipation (or, conversely, in heat conservation) of urban birds.

CHAPTER VI.
URBAN NESTLINGS HAVE REDUCED NUMBER OF FEATHERS IN GREAT TITS

Abstract

The plumage of birds plays an essential role in thermal insulation and influences the heat tolerance of birds. These plumage functions are mainly determined by the number and density of feathers, but it is unclear how feather density responds to environmental changes in wild populations. In urban birds, both high temperature and limited food could generate changes in plumage traits. To investigate the effect of urbanization, we compared the number of feathers on the sternal region of nestlings between urban and forest great tits using a novel non-invasive method. We showed that 6-9 days old urban nestlings have fewer feathers than forest nestlings. Although the density of feathers was slightly higher in urban nestlings, this was the result of the smaller size of their feather tracts. We suggest that the reduced feather number may be the result of adaptation to higher urban temperatures and/or constrained feather development due to the limitation of optimal nestling-food sources in urban environments. Concentrating body feathers in a reduced tract area may also help birds to adapt to higher urban temperatures because this can increase the relative size of bare body surfaces which may facilitate heat dissipation. We suggest several possibilities for future studies that would help to disentangle the underlying mechanisms responsible for the observed patterns.

This chapter is a modified version of the research article: Sándor, K., Liker, A., Sinkovics, Cs., Péter, Á., Seress, G. (2021). Urban nestlings have reduced number of feathers in Great Tits (*Parus major)*. *Ibis.* DOI: https://doi.org/10.1111/ibi.12948

6.1. Introduction

In birds, besides a range of physiological, behavioural, and some morphological mechanisms (Tattersall *et al.* 2012, Ryeland *et al.* 2017, Thompson *et al.* 2018), the plumage also plays a key role in regulating body temperature by facilitating or constraining the extent to which heat is retained close to the body (Wolf & Walsberg 2000). This, in turn, is determined by several properties of the plumage, such as the structure, number, and density of body feathers (Wolf & Walsberg 2000, Jiang *et al.* 2010, Grémillet *et al.* 2012). Feathers grow in distinct feather tracts (Clench 1970) in which the formation of feather follicles takes place during embryonic development (Yu *et al.* 2004) – thus the maximum number of feathers a bird can develop is fixed at hatching. Interspecific comparative studies demonstrated that the variation in the number and density of feathers is related to habitat type (Osváth *et al.* 2018), diet (Osváth *et al.* 2018), body size (Hutt 1938, Møller 2015), and migration distance (Møller 2015). Two recent studies also suggest negative correlations of the ambient temperature of the species' environment with the feather number (Møller 2015) and feather density (Osváth *et al.* 2018). However, much less is known about how these traits vary within a species. Experimental work in captive poultry suggests that both the food availability of egg-laying females (Dahlke *et al.* 2008) and the incubation temperature of eggs (Scott *et al.* 2015) affect the number of follicles formed in embryos. While the few within-species studies on wild birds also suggest the influence of temperature and food availability on feather structure (Pap *et al.* 2008, Broggi *et al.* 2011), it is virtually unexplored how other plumage traits like feather number and density differ between wild populations living under different environmental conditions.

The urban environment provides a great opportunity to examine the adaptability of these properties on wild animals. On the one hand, the altered food palette (lower quality and quantity of natural food sources, like insects, but higher amount of anthropogenic food sources; for more details see ***Chapter I***, section *1.1. Food limitation in urban habitats*) in urban habitats may influence the quality and number of developing body feathers, for example through its effects on the pre-breeding condition of egg-laying females (for similar carry-over effects of food quality on egg and nestling quality see Plummer *et al*. 2013a, 2013b). While suboptimal food is known to affect, for example, plumage coloration in wild birds (Eeva *et al.* 2009, Isaksson 2009), its impacts on the thermoregulatory properties of the plumage are unexplored.

On the other hand, the altered microclimate (high temperatures, more frequent heat days and milder winters; for more details see ***Chapter I***, section *1.2. Urban heat island*) of cities may also influence the thermoregulatory properties of plumage of urban birds. Indeed, the effects of

the UHI (***Chapter I***, section *1.2. Urban heat island*) have already been documented in a wide range of organisms (Parris & Hazell 2005, Jochner & Menzel 2015, Diamond *et al.* 2017, Merckx *et al.* 2018) including birds (Pipoly *et al.* 2013, Rodríguez & Barba 2016). Recent studies also found adaptive responses to the elevated temperature in some urban populations (Brans *et al.* 2017, Diamond *et al.* 2017), but such responses regarding avian plumage have not been described yet.

In this study, we compared the number and density of contour feathers between nestlings at two urban and two forest habitats that differ in their ambient temperature and natural food supply (for more details see: Appendix *A/III.1. Temperature* and *A/III.2. Food availability*). To achieve this, we developed a novel method that is, contrary to the former studies (e.g. Wetmore 1936, Osváth *et al.* 2018), non-invasive (i.e., it does not require the plucking of birds' feathers) and can be applied on living specimens (nestlings at an early age). We predicted fewer feathers and lower feather density in urban compared to non-urban nestlings because of at least two, mutually non-exclusive reasons. First, because both traits might be adaptive to UHI (e.g. to decrease the risk of heat stress during the nestling stage; Speakman & Król, 2010), and second, because feather development of offspring may be constrained by the suboptimal feeding conditions met by egg-laying urban females (see above).

6.2. Methods

6.2.1. Fieldwork

We carried out our study in April-May 2018 in two urban (Veszprém and Balatonfüred) and two forest (Vilma-puszta and Szentgál) great tit populations (for a detailed description of study sites see ***Chapter III***). From egg-laying, we monitored nestboxes at least twice a week (and more frequently during the expected time of hatching) to determine the exact hatching date (day of hatching = day1). We collected feather number data when nestlings were 6-9-days old (urban nestlings, *mean* ± *SE*: 7.4 ± 0.1 d, forest nestlings: 7.3 ± 0.1 d). This age range represents an optimal developmental stage for this measurement because feathers have already emerged from the skin within the main feather tracts (pers. obs.) but they are still covered by sheaths – thus, in this stage, feathers do not overlap and can be counted accurately (Figure VI.1a). To further increase the precision of our measurements, on the day of sampling we always chose nestlings that were in the optimal feather development stage for the purpose of our measurements. Note that in some nests, this selection method resulted in choosing nestlings with less developed plumage, while in others, it resulted in choosing nestlings with moderately or even the most

developed feathers (this mostly depended on the age of the broods, as nestlings' plumage develops significantly day by day at this stage). Thus, the selection of nestlings from a brood was not completely random due to this methodological constraint. However, since there was no overall habitat difference in the sampled broods' age (see above), it is not likely that this selection method could have influenced our habitat comparisons.

From the nestlings in optimal plumage condition, we randomly selected three per brood and took close-up photographs on their sternal region of the ventral feather tract by gently stretching chicks a bit by their legs and heads (Figure VI.1a). Before taking photos, we attached a millimeter scale (20×10 mm) to the nestlings' belly next to the examined feather tract (Figure VI.1a); this label contained nestling ID and served as a reference scale during photo processing (see below). When taking photos, the camera lens was always parallel with the scale and the feather tract. Nestlings' body mass was measured with a Pesola spring balance (± 0.1 g). We decided to sample only 3 chicks per nest rather than studying whole broods because this procedure took several minutes per chick, which would have meant a significant amount of extra disturbance in large broods that we certainly wanted to avoid.

6.2.2. Measuring feather traits on photographs

To extract data from the photographs we used ImageJ (v. 1.51). First, we determined the scale for each photo by using the attached millimeter scale. Second, we outlined the area of the ventral feather tract as follows (Figure VI.1a). At the neck, we determined its borderline by following the feather tips of the crosswise feather row, starting at the point where the feather tract of the wing intersects with the ventral feather tract (Figure VI.1b). On the sternal side, the borderline followed the feather tips of the 7th row of feathers (rows counted from the lateral edge of the feather tract, Figure VI.1c). We chose this method based on our prior observations, which showed that the sternal and abdominal feather tracts of great tits in both habitats typically differentiate at the 7th and 8th feather tracts. Finally, at the lateral and the posterior ends of the tract we followed the tips of the most exterior feathers (Figure VI.1a). Next, within this area, we counted the number of contour feathers (henceforth 'feather number'), and also measured the size of the outlined body surface area (mm2, henceforth 'area') and the length of the three longest feathers (mm, henceforth 'feather length'). Then we calculated the density of contour feathers as feather number divided by the area (henceforth 'feather density'). The final sample involved 95 urban (Veszprém n = 60, Balatonfüred n = 35) and 73 forest (Szentgál n = 54, Vilma-puszta n = 19)

nestlings (from 42 urban and 29 forest broods; for details, see Appendix *A/III.3. Feather measurements*).



Figure VI.1. Measuring feather traits on photographs. (a) The examined area of a nestling's ventral feather tract with the millimetre scale as reference. (b) The position of the anterior borderline (white line) is determined by the intersection of the wing's feather tract with the ventral feather tract (white arrow) and follows the feather tips of the crosswise feather row (white ellipse). (c) The sternal borderline (white line) was determined at the tips of the 7th row of feathers counted from the lateral side of the feather tract.

6.2.3. Statistical analyses

First, we tested between- and within-measurer repeatability by intraclass correlation (function '*ICC'*, package *'irr'*). The repeatability was high for all variables both between and within observers (for more details see Appendix *A/III.3. Feather measurements*). Next, to test our predictions for the effects of habitat type on feather tract traits, we followed the approach suggested by Ruxton and Beauchamp (2008) and conducted pre-planned comparisons between the study sites in two steps (similarly to ***Chapter IV,*** section *4.2. Methods* and ***Chapter V,*** section *5.2. Methods*) . In the first step, we identified significant confounding variables besides the effect of the main predictor (study site). Thus, we fitted three separate linear mixed-effect models (*LME*, package *'nlme'*, with Gaussian error distribution) for nestlings' feather traits (feather number and density), and also for area. These models included study site as main effect (four levels) and the following predictors: body mass to control for nestlings' condition (in feather number model) or to control for their body size (because heavier nestlings are bigger; in the area and density models); feather length to control for its effects on the accuracy of feather counting

(longer feathers might cover each other; in feather number model) and area measurements (because feather tract was outlined along the feather tips; in the area and density models); and clutch size (as feather follicles are formed during embryonic development; in feather number model) or brood size (in the area and feather density models) to take into account the potential trade-off between clutch or brood size and nestling quality. We included nest ID as a random factor in all models. Note that fitting these models is a necessary first step for the main analysis of the study, the calculation of linear contrasts, so we did not base the conclusions of our study on these models.

In the second step, we conducted pre-planned comparisons (regardless of the results of the first stage analysis) to compare the means of the three response variables between habitats. We used separate linear models for each response variable that contained study site (four levels), and significant ($p < 0.05$) predictors from the full LME models described above. Note that all the included covariates were statistically significant (Table VI.1a), except for clutch size in the feather number model (ANOVA, $\chi_{2(1)} = 0.267$, $p = 0.605$) and brood size in the area ($\chi_{2(1)} = 0.643$, $p = 0.423$) and feather density ($\chi_{2(1)} = 0.394$, $p = 0.530$) models that were thus not retained in the final models. Then we calculated linear contrasts from each model's estimated marginal means (package *'emmeans'*) between the two habitat groups (i.e. differences between the two urban and the two forest sites). We conducted all analyses in R (v. 3.6.2, R Core Team 2019). We checked assumptions of residuals' normality and homogeneity of variance by inspecting the residuals plots for each model, and also calculated *VIF* values (package *'car'*), which indicated low collinearity between variables (*VIF* < 2.18) in all cases.

6.3. Results

Linear contrast analyses confirmed habitat differences: on their sternal region, urban nestlings had significantly fewer feathers and higher feather density than forest nestlings (Table VI.1b). We also found smaller feather tract areas in urban nestlings and this difference was significant after controlling for the effects of body mass and feather length (*contrast* ± *SE:* 3.59 ± 1.58, $t = 2.270$, $p = 0.026$).

Table VI.1. Results of (a) the full LME models on factors affecting feather number and density (number/mm^2) in great tit nestlings, and (b) habitat differences in these traits. The linear contrasts compare the two forest sites to the two urban sites, positive values indicate higher values in forest nestlings. Statistically significant ($p < 0.05$) differences are highlighted in bold.

	(a) Final models			(b) Forest – urban contrasts			
	df	χ^2	*p-value*	*contrast ± SE*	*df*	*t ratio*	*adjusted p-value*
Feather number							
Site	3	24.228	**<0.001**	2.91 ± 0.87	67	3.347	**0.001**
Body mass	1	6.151	**0.013**				
Length	1	7.104	**0.007**				
Density							
Site	3	10.580	**0.014**	- 0.08 ± 0.039	67	-2.082	**0.041**
Body mass	1	24.427	**<0.001**				
Length	1	113.617	**<0.001**				

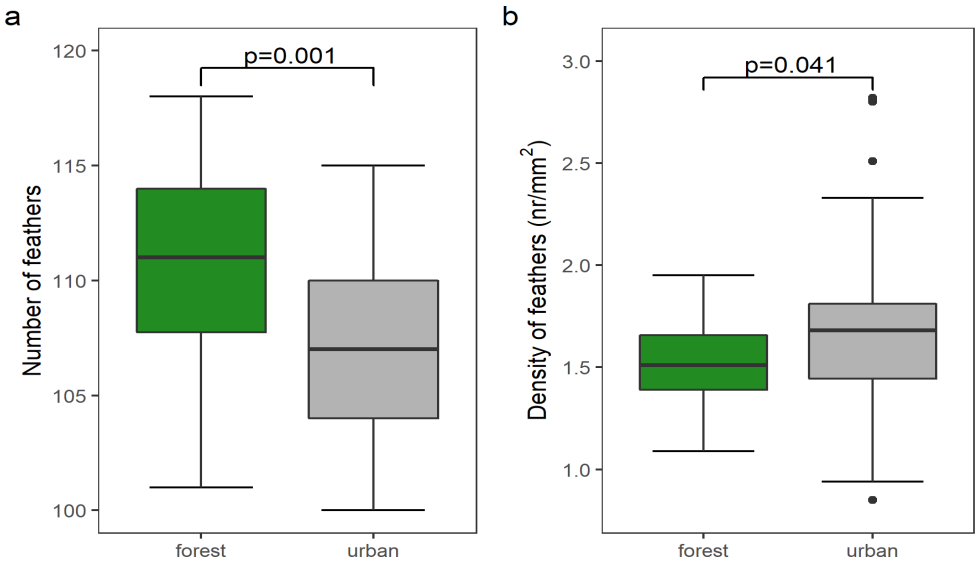


Figure VI.2. Habitat differences between number (a) and density (b) of contour feathers between 6-9 days old forest and urban great tit nestlings. Medians, interquartile ranges and data ranges are shown by the middle thick lines, the boxes, and the whiskers, respectively.

6.4. Discussion

In urban areas, ecological factors like climate or food quality are significantly altered, and these changes can contribute to the differences in traits between urban and non-urban animal populations – through either adaptation or developmental constraints. In this study, we compared birds' feather number and density, i.e. traits that can strongly influence the insulation properties of plumage, between two urban and two forest habitats that greatly differ in their ambient

temperature and natural food supply. To our knowledge, this is the first study that investigates the between-population variation of these traits in a wild bird species, and also the first that does so in an urbanization context. To achieve this we developed a novel, non-invasive, and easily applicable method with high repeatability that, contrary to former methods, can be applied to living birds. Therefore, compared to earlier, more opportunistic sampling methods (e.g. Osváth *et al.* 2018), this new approach allows more systematic data collection with which larger amounts of data can be collected from several individuals from a targeted location.

Our result that nestlings had significantly fewer contour feathers in the urban (i.e., warmer) environment. This result is in line with our expectations and also corroborates the findings of Møller (2015) who showed a negative correlation between feather number and seasonal temperature (that is, birds have more feathers during autumn and winter, followed by a gradual feather loss during spring and summer until the next annual moult). Several mechanisms can contribute to reduced feather numbers in urban birds, as detailed below.

Firstly, since feather density is a heritable trait (e.g. a moderate heritability was found in domestic chickens, Sun *et al.* 2019) differences between populations may be based on genetic differences due to selection favoring the tolerance of higher ambient temperatures in urban areas (as in our study system; Appendix *A/III.1. Temperature*). For example, it is well-known in poultry that fewer feathers (like in naked-neck broilers) are advantageous under high temperatures (Deeb & Cahaner 1999), allowing easier heat dissipation, thereby enhancing heat stress tolerance (Jiang *et al.* 2010). On the same basis, increased ability of heat dissipation could also be beneficial for wild urban birds. This might especially hold for altricial bird species like great tits whose nestlings are exposed to the prevailing ambient temperatures in the nest, and do not have established competent thermoregulation in their early life, thus might be sensitive to the harmful effects of UHI during summer heat days (Rodríguez & Barba 2016, Andreasson *et al.* 2018). As Pipoly *et al.* (2022) showed, heat days (>28.7°C) are indeed significantly more frequent at our urban compared to forest sites during the chick-rearing period: in 2013-2018 (six years) 45.9% of the urban broods experienced at least one heat day (range: 1-13 heat days per brood), while this rate was only 20.8% in the forest sites (range: 1-5 heat days per brood). High temperatures can be especially problematic for hole-nesting species breeding in artificial nestboxes, as the temperature of the cavities and nestboxes can be up to several degrees higher than the ambient temperature (Maziarz *et al.* 2017). The microclimate of the nest can therefore further enhance the effects of the UHI, which the nestlings have to cope with. Although 8-10 days old altricial nestlings are already capable of active heat dissipation by panting (hence regulating their body temperature to some extent, Andreasson *et al.* 2018), this can be costly as panting is associated

also with intense water loss (Wolf & Walsberg 1996). In natural habitats, this cost can be effectively compensated by consuming food with high water content, like caterpillars (Zandt 1996). In urban areas, however, the scarcity of such prey items (Seress *et al.* 2018) might significantly increase the cost of this behavior, thereby increasing the relative role of plumage in the dissipation of extra heat for urban nestlings. Note that the brood size may also influence nestlings' capability of thermoregulation and heat dissipation, because smaller compared to larger broods can cope with high temperatures more effectively and the converse is true for low temperature (Mertens 1977, Andreasson *et al.* 2016). In our urban great tit populations, similarly to other studies, broods are consistently smaller than in the forest populations (Seress *et al.* 2018) a pattern that was also present in the current study (*mean* ± *SD*, number of hatchlings, urban: 8.0 ± 1.9; forest: 10.3 ± 1.9; number of 14-16 days old nestlings, urban: 6.5 ± 2.9; forest: 9.4 ± 2.4). Thus, smaller brood size in urban habitats may also contribute to the thermal tolerance of nestlings, potentially helping them to cope with the elevated nest microclimate in cities. Having fewer feathers, however, could also be advantageous for adult urban birds when coping with elevated summer temperatures (Grémillet *et al.* 2012, Nilsson & Nord 2018, Nord & Nilsson 2019, Tapper *et al.* 2020) in cities, while the reduced insulation capacity is probably less costly in winters due to the relatively milder climate in temperate zone cities (Hinkel *et al.* 2003).

Secondly, fewer contour feathers could be the result of environmental constraints taking effect during embryonic development, when the number of follicles (hence feather number) is determined (Yu *et al.* 2004). For example, due to the low availability of optimal food sources in cities (see Appendix *A/III.2. Food availability*), females may be constrained from laying high-quality eggs (Toledo *et al.* 2016), resulting in suboptimal nutrition for embryos' development (Krist 2011), hence affecting feather follicles' formation (Scott *et al.* 2015). Note that growing fewer feathers can be beneficial in poor nutritional environments because it reduces the energetic costs of feather development, and this energy can be invested into other essential traits like immune functions (Moreno-Rueda 2010). Finally, nest microclimate during the incubation of eggs may also affect nestlings' phenotype through developmental plasticity, as suggested by a study on blue it *Cyanistes caeruleus* that found reduced tarsus length in nestlings under experimentally elevated incubation temperatures during the egg stage (Nord & Nilsson 2011). Thus, it is conceivable that higher incubation temperatures in urban nests could also contribute to the lower feather number of urban nestlings in some extent.

We found a higher contour feather density in the sternal region of urban nestlings, which seemingly contradicts our prediction and also the results of former studies documenting lower feather densities in warmer environments (Jiang *et al.* 2010, Osváth *et al.* 2018). The higher

feather density in urban nestlings, however, was the result of their smaller feather tract area. Importantly, this habitat difference in feather tract area remained significant even after we controlled for the effect of body mass, meaning that nestlings with the same weight had disproportionally smaller feather tract areas in urban compared to forest broods. In theory, one explanation for the observed habitat difference may be that the body density is higher in urban than forest nestlings, for example, due to their lower amount of fat reserves. However, the broods involved in our study do not show habitat differences in fatness at ringing (for more details see Appendix *A/III.4. Nestling fat score*). Consequently, urban nestlings seem to have a relatively smaller feather-covered body surface compared to forest nestlings that can also be beneficial in terms of more effective heat dissipation (Speakman & Król 2010, Grémillet *et al.* 2012, Nilsson & Nord 2018). Thus, it is possible that urban birds can achieve increased heat tolerance not only by reduced feather numbers but also *via* relatively larger bare body surfaces.

Finally, it is also important to note that 6-9-days old nestlings are still in development (Tilgar & Mänd 2006). While their body size is increasing day by day, the number of their contour feathers is not (as the number of feather follicles are fixed hatch, see the introduction), which may result in a decrease in feather density throughout their nestling stage. However, how these traits ultimately affect insulation and thus thermoregulation in adults, is still an open question and requires more research. Furthermore, it should be noted that we examined the ventral feather tract, which constitutes a significant portion of the plumage but not the entire plumage. It is possible that the observed habitat differences may manifest differently on the other parts of the plumage. Therefore, it would still be worthwhile to investigate whether the differences observed here can also be found in the other feather tracts.

Although our study is of correlative nature, it points to a previously undescribed effect of urbanization on birds' morphology. Interestingly, our two urban study sites are relatively small and green, temperate-zone cities, and yet these areas, when compared to their surrounding natural habitats, are already 'urban enough' to exhibit significant differences in local climate and birds' natural food supply along with the plumage traits of great tits. Therefore, it can be expected that the changes we found in feather number and density are likely to be more pronounced in more heavily urbanized regions, resulting in more important fitness consequences to 'big city birds'. Thus, in the future, it would be interesting to carry out similar studies in more heavily urbanized areas or to measure the ratio of bare and feathered body surfaces in urban and non-urban conspecifics. Studying the effects of urbanization on the structural properties of contour feathers could also be an interesting next step. For example, changes in the density or proportion of the plumulaceous part in contour feathers (which also contributes to the thermal insulation of birds)

could strengthen or contrarily, compensate for the effects that fewer feathers pose on urban birds' thermoregulation (Pap *et al.* 2017). Since both adaptation and constraints can explain our results, further experimental studies, such as food supplementation of egg-laying females, or heat treatment of eggs during the incubation period could help to disentangle the background mechanisms. Finally, it is also important to consider that behavioral changes (Pattinson *et al.* 2020), smaller brood size (Mertens 1977), and smaller body size (Merckx *et al.* 2018) may also help birds to tolerate elevated temperatures in urban habitats.

CHAPTER VII.
GENERAL DISCUSSION

In my PhD work, I studied the effects of the urban environment on the development and plumage characteristics of a common urban bird species, the great tit. In this chapter, I summarize my main results and I suggest some potential directions for future studies in these research topics.

Food limitation in the city

To better understand how certain environmental factors affect living organisms, it is very important to carry out field and laboratory experiments in which the effects of different factors can be investigated under fully or partially controlled conditions. Several urban ecological studies found that urban birds were less successful in several respects than their non-urban conspecifics. For example, urban birds usually have smaller clutches, smaller nestlings and lower fledging success (Meyrier *et al.* 2017, de Satgé *et al.* 2019, Corsini *et al.* 2021), thus having a lower overall reproductive success. This is probably mainly due to one of the most fundamental anthropogenic effects, the altered food availability for birds in urban environments. However, most of the earlier studies were correlative, e.g. compared reproductive success between different areas that vary in the degree of urbanization, that probably differed from each other in many ecological conditions besides food availability. Surprisingly, there are still very few experimental studies on this topic (e.g. Bańbura *et al.* 2011, Demeyrier *et al.* 2017, Meyrier *et al.* 2017), these produced conflicting results, and were often not controlled for important confounding factors. Therefore, I intended to fill this knowledge gap with the food manipulation experiment presented in ***Chapter IV***. My results clearly showed that food limitation during the breeding season is a major challenge for urban birds in our study system. I found that urban nestlings greatly profited from the supplementary food because by the end of the nestling development period they either caught up with (e.g. in tarsus length and survival) or were very close (e.g. in body mass and wing length) to their forest conspecifics. These results suggest that in our study system, food limitation in the urban environment has probably one the strongest negative effect on the success of urban birds from the earliest stages of their lives.

In a recent study of the same great tit populations, Sinkovics *et al.* (2021) showed that there are significant differences in the composition of prey items provisioned to urban compared to forest nestlings. Their results are in line with other previous studies, such as Pollock *et al.*

(2017), Jarrett *et al.* (2020), Senar *et al.* (2021). These studies found that, compared to forest broods, urban nestlings' diets contain lower proportions of caterpillars (the most preferred prey type of many insectivorous birds, that has the highest nutritional value; e.g. Eeva *et al.* 2010) and a higher proportion of non-arthropod food items (like sunflower seeds and anthropogenic food that is known to be suboptimal for nestling development). Furthermore, Sinkovics *et al.* also studied the amount (volume) of the provisioned prey items, which is a much less well researched factor than the composition of nestlings' diet. This study showed that the average volume of prey items was smaller in urban than in forest broods, but there was no habitat difference in the total volume of food received by a nestling during a one-hour observation. This result suggests that parent birds were able to quantitatively compensate for the small prey size with increased feeding activity, with the result that urban nestlings receive more but smaller prey items per capita. Urban parents' increased nestling-feeding effort to quantitatively compensate for the caterpillar shortage is not sufficient, however, as indicated by the fact that urban broods experienced lower breeding success in all study years, especially in those with low caterpillar availability (for more details see Sinkovics *et al.* 2021). These results further corroborate that the suboptimal composition and nutritive value of nestling food is a strong limiting factor for urban birds' reproductive success. The composition of the nestlings' diet, however, highly depends on the abundance and biomass of available insects, which is known to be significantly lower in urban habitats (Merckx *et al.* 2018, Fenoglio *et al.* 2020).

One of the main reasons for the lower arthropod availability in cities is the reduced size of the urban green spaces and the unfavorable composition of plants (Narango *et al.* 2018). The diversity of plants in cities are usually very high, but a significant proportion of these are introduced, non-native species. From an ecological point of view, the main problem with this exotic vegetation is that it supports a less abundant, and less diverse phytophagous arthropod community (e.g. reviewed by Tallamy *et al.* 2020) compared to native vegetation. For example, it is known that many herbivorous insects specialize quite strongly on one or a few host plants (Forister *et al.* 2015), so newly introduced plants are usually not a suitable habitat for them. Therefore, although these plants may be desirable from an aesthetic or urban planning point of view (e.g. they are easy to maintain), they do not actually provide adequate feeding grounds for insectivorous and other birds species that feed their nestlings with arthropods (Narango *et al.* 2017, 2018, Tallamy & Shriver 2021). This, in turn, may lead to the decline of bird populations or even the disappearance of some species from the urban environment. On the other hand, the highly altered arthropod communities in cities may force urban birds to specialize to a certain extent on the food sources available in their territories (Pagani-Núñez *et al.* 2015), for example,

by using a higher proportion of anthropogenic food sources, to forage on a larger area (resulting in larges flight distances during the nestling-rearing period; Jarrett *et al.* 2020) and/or to increase their feeding activity (e.g. as seen in Sinkovics *et al.* 2021).

If we want to make our cities bird-friendly, it would be necessary to plant and maintain (preferably native) plant species that can withstand the effects of the urban environment (e.g. different types of pollutions, increased frequency of heat stress), but most importantly, that can support rich arthropod fauna as well. The latter can be assessed by using different types of insect and frassfall traps (that can be used to determine the biomass of defoliating communities; e.g. Hallmann *et al.* 2017, Seress *et al.* 2018, Harris *et al.* 2019), but this would be indirect information about the available prey, and it does not necessarily reflect the preferences of birds. Another and more direct information could be acquired by observing the foraging behavior of nestling-feeding parents to better understand which plant species they prefer and how effectively they can forage on these substrates. Trying to answer this latter question, in 2021 we performed a follow up field study in which we applied radio telemetry transmitters on breeding female great tits that enabled us to monitor their fine-scale foraging behavior and territory use in detail to see e.g. how far they go from the nestboxes for nestling food, and what their preferred plant species and other foraging grounds are. We also combined radio-telemetry tracking and field observations with video cameras mounted on the nestbox, to record parents' nestling-provisioning activity. From these video records, we will be able to determine the type of prey items brought from the observed foraging sites (Sinkovics *et al.* 2018). By comparing the data of the tree species used by these females with all of the trees (number and the volume of trees belonging to different species) available on their territory, we can calculate their preference for certain species (Bjørneraas *et al.* 2012). Combining this data with the type and size of the provisioned prey items, we can get a deeper insight into which plant species are the most useful for nestling rearing birds in cities (this study is currently in progress).

Changes in the plumage in urban birds

In the second part of my PhD work, I focused on the plumage traits of birds. Because plumage has a diverse function in birds' life, it is important to better understand how the urban environment affects the different types of feathers that, in turn, may significantly increase (through adaptation) or decrease (through constraints) the success of birds in cities. Thus, studying plumage could be an important component to expand our understanding of the complex

effects of urbanization on birds. In my studies, I aimed to take the first steps to fill this knowledge gap.

The fine-scale comparison of urban and forest great tits' feather structure (***Chapter V***) yielded two main results. First of all, I found significant differences in wing and contour feathers, but these were present only in the plumage of FY (first year) birds. As I have shown in ***Chapter IV***, the development of urban nestlings is significantly affected by their suboptimal food, so it is not surprising that this is partly reflected in the quality of their plumage as well. This was my main explanation for the observed differences in wing feather structure between urban and forest FY birds. If these differences are indeed the result of food limitation, it can be assumed that these feathers are of lower quality than in forest birds. This, in turn, can have carry-over effects during the subsequent life stages (Minias *et al.* 2015). For example, during their first few weeks after fledging birds are inexperienced, and their flight capabilities are lower. During this critical period, fledglings with lower quality wing feathers may have altered flight abilities that also have a significant impact on their survival.

The other main result of this study was that the structure of contour feathers also differed between urban and forest birds. This result could be primarily explained by adaptive processes that are possibly caused by the warmer microclimate of cities. If this is the case, the observed changes in contour feathers of urban FY birds may help them to cope (through a better heat dissipation) with warmer temperatures during the first part of their lives.

Since ***Chapter V*** is a descriptive study, I don't know the exact causes of the observed differences between urban and forest birds' feather structures. To understand these processes, as a first step, we would need a much deeper knowledge of how different environmental factors affect different types of feathers, and how these changes affect the functions of feathers. As I emphasized in ***Chapter V***, feather structure studies still suffer greatly from the lack of an experimental approach. In addition, most of the studies on this topic use different methods to quantify the properties of feathers, which makes it very difficult to compare and comprehensively interpret their results. Therefore, more experimental studies (with comparable methods) are needed to advance our understanding. For example, a food manipulation experiment (with a similar design to the experiment I presented in ***Chapter IV***) could be useful to assess whether and how supplemental food affects the structure of feathers in FY birds, especially in the urban environment. If supplemental insect food would eliminate the difference in wing feathers between urban and forest FY birds, this would be a strong support for the idea that these plumage differences are indeed caused by the suboptimal diet. Similarly, the effects of the urban heat on

the contour feathers could be experimentally tested by manipulating the microclimate of the nestboxes before or during the nestling rearing period. If the structure of contour feathers changes plastically due to the thermal conditions experienced before or during the nestling phase, I would expect significantly less dense contour feathers in heat-treated groups in both urban and forest birds compared to untreated groups. However, if the structure of contour feathers is a mostly genetically fixed trait, then I expect that the effect of the heat treatment would be small among these groups.

The difficulty of both food manipulation and heat treatment experiments would be that the feathers of nestlings before fledging are not yet suitable for feather structure measurements as they have not yet fully developed, thus it can result in misleading conclusions. Therefore, birds belonging to the involved broods would have to be recaptured after they fledged (preferably after their post-juvenile moult), but before their first post-breeding moult. This would require a high effort on the field, however, because it is difficult to sample a sufficient number of birds due to both the dispersion of young birds and their high post-fledging mortality.

Another possibility to study the carryover effects of ambient temperature on contour feathers is to examine whether the temperature conditions experienced during the nestling phase correlate with the structural properties of these feathers. This could be performed on FY birds that were hatched and ringed in our nestboxes, thus both their hatching and fledging dates (i.e. their growing period) are exactly known. Based on these data, various types of relevant temperature information (e.g. average temperatures and the number of heat days; for more details see Pipoly *et al.* 2022) can be accurately collected and compared to plumage characteristics, but the results of this study will refer to the plumage state acquired after the post-fledging moult.

It remains an open question whether and how the observed feather structures of urban FY birds affect the functioning of the plumage. The aerodynamics of wing feathers and its effects on flight performance (e.g. wingbeat amplitude, energy gain, acceleration: Williams & Swaddle 2003; and maneuverability; Swaddle *et al.* 1996) of FY birds could be tested in narrow aviaries, where the kinematics of birds' flight could be analyzed by using high-resolution cameras and motion-analysis systems. Furthermore, the differences in the functions of contour feathers with different densities could also be tested in aviaries, under controlled conditions. In the past, the heat transfer capacity of plumage was measured primarily on the skin of dead birds (Walsberg 1988, Ward *et al.* 2001, and also Graveley *et al.* 2020), which had the clear advantage of being able to control all other confounding factors that can also contribute to the thermoregulation of birds (like physiological processes, body size, fat thickness and other individual differences).

However, with modern devices, these measurements can be performed non-invasively on living subjects, for example by using infrared thermal imaging cameras (that are already used e.g. to measure the body temperature of broilers on their bare body parts; Bloch *et al.* 2020). This could be done simply by measuring the surface temperature of the plumage with these cameras along with the body temperature of the birds at a controlled ambient temperature (e.g. in neutral and warm conditions), which would provide information on how much heat is dissipated through the plumage with different contour feather densities.

During my PhD work, I also examined the effects of the urban environment on plumage with another approach, by focusing on the number and density of contour feathers covering the body and the size of bare body surfaces (***Chapter VI***). In this study, I found some substantial differences: urban nestlings had fewer feathers and smaller feather tracts on their sternal regions (suggesting larger bare body surfaces) than their forest conspecifics. These results can be also explained both by food limitations (in this case in the egg-laying females) and adaptations to the urban microclimate. As this is also a correlative study, I cannot learn exactly to what extent these factors contribute to the observed differences. Testing of these can be also done by food and/or heat manipulation experiments in both urban and forest habitats, but in this case, these should be done before the time of hatching. To test whether the food limitation is the main driver of fewer feathers in urban birds, the food manipulation experiment should start weeks before the eggs are laid, to ensure that the egg-laying females can allocate the proper amount and quality of nutrients into the eggs. This can be done by providing supplementary food on nestboxes in areas where we observe birds showing territorial behavior before starting to breed. In this experiment, it would be very helpful to carry out the study in territories where at least the females are color ringed to be sure that the same bird consumed the extra food whose brood will be examined in the next weeks. Alternatively, the effects of temperature on the number of feathers and size of bare body surfaces can be tested during de embryonic development phase by placing heating pads under the nest material (Álvarez & Barba 2014) to artificially elevate the inner temperature of nestboxes during this phase. If these experiments result in the elimination of the differences between urban and forest nestlings, it would indicate that the studied plumage traits are plastically determined by the food limitation of egg-laying females and/or temperature conditions during embryonic development. However, if these differences still remain after the treatments, it would suggest that the plumage characteristics studied in ***Chapter VI*** of urban birds are the result of a genetically fixed adaptation.

As I mentioned in ***Chapter VI,*** based on previous studies, fewer feathers and larger bare body surfaces observed in urban birds are likely to significantly aid heat dissipation (Deeb &

Cahaner 1999, Jiang *et al.* 2010, Nord & Nilsson 2019), which is beneficial in a warm urban environment. These results are consistent with the differences in contour feathers of FY birds presented in ***Chapter V***, as both structural properties and plumage characteristics change in the same direction: resulting in a looser structure of plumage in urban birds. At the same time, the differences observed here partly complement the results of ***Chapter V***: fewer feathers and larger bare body surfaces may be more advantageous in terms of adapting to the warmer urban microclimate than changes in feather structure – this may explain why there are no significant differences between the structures of contour feathers of urban and forest AFY great tits. But it is still an open question whether the differences observed between urban and forest nestlings persist into adulthood. Due to methodological reasons, I performed this study only on nestlings, thus I can only partially know what differences may exist between the two habitats' birds in adulthood. On the one hand, it is known that the number of contour feathers does not change after hatching, so these differences persist into adulthood. On the other hand, there is no information on how the size of feather tracts changes as birds grow, so it's not sure whether there are differences in the size of bare body surfaces in adulthood. To examine this, it would be needed to use the earlier methods, and measure these traits on dead birds (Hutt 1938, Scott *et al.* 2015, Osváth *et al.* 2018). In addition, the amount of downy feathers (which also play a role in thermoregulation) could be examined on dead birds, which is not yet visible at the age of 6-9 days, but appears on different body parts by adulthood. For this, however, it is difficult to collect a large number of naturally dead individuals from these habitats on which a reliable analysis could be performed to test habitat differences. However, an interesting new study could also be the comparison of the heat dissipation capability of urban and forest birds. This can be done by using thermal imaging cameras as suggested above. As I have shown in ***Chapter V,*** the contour feathers of urban and forest FY birds differ significantly, while there is no difference between AFY's feathers, therefore these age groups should be tested separately. If the results would show different rates of heat dissipation between urban and forest AFY birds, it would indeed suggest that the heat dissipation of urban AFY birds is primarily provided by the fewer feathers and/or larger bare body surfaces.

My results show diverse effects of the urban environment on birds, in which different constraints and adaptation processes may play significant roles. In addition, my results open up several new questions, also serving as a basis for much future research on this topic. Through these, we can better understand how and to what extent urban-living birds can adapt to this new environment, and how we can help them to thrive in our highly transformed environments in the future.

THESIS POINTS

Food availability limits avian reproduction in the city: an experimental study on great tits

1. I investigated the effects of the food limitation in urban environment on the reproductive success of urban birds. I showed that the urban nestlings that did not receive supplemental food in a field experiment had significantly smaller body sizes and lower survival rates than non-supplemented nestlings in the forest. However, these habitat differences almost completely disappeared when urban broods received supplementary food: supplementary fed urban nestlings had similar body sizes and survival rates to those of control broods in the forest environment. In contrast, food supplementation in forest broods had small and non-significant effects on these traits. These results provide one of the strongest evidence that food limitation is primarily responsible for the smaller body size and reduced reproductive success of urban birds.

Differences in feather structure between urban and forest great tits: constraint or adaptation?

2. I compared the structural properties of contour feather of urban and forest birds. I found that the urban environment only affected the contour feathers of first year old birds, while I did not find any difference in adults. The urban first year great tits had contour feathers with lower densities, which ultimately provides a looser plumage structure in these birds. Although it is not entirely clear from the interpretations of previous studies how different densities of feathers affect the thermal insulation, I assume that in the studied urban populations the looser plumage provides better heat dissipation for birds. These changes in contour feathers are probably driven by the adaptation to the warmer climate in cities.

3. I also compared the structural properties of flight (wing and tail) feathers between urban and forest birds. I did not find any habitat differences in adult birds, however, I detected differences in two traits of wing feathers in first year birds. Based on the results of previous studies, these changes may negatively affect the flight performance of first year birds, which may ultimately affect their chances of survival until their subsequent moult. The habitat differences in wing feather structure may be explained by the effects of several environmental constraints, for example the poorer quality of food available to insectivorous birds in the urban environment.

Urban nestlings have reduced number of feathers in great tits

4. I investigated the differences in the number of contour feathers and the density of plumage between urban and forest great tit nestlings at the age of 6-9 days. I found that urban nestlings had significantly fewer feathers and smaller feather tract area (probably implying larger bare body surfaces) than forest ones. This latter finding may indicate an adaptation to the warmer urban microclimate, as bare body surfaces can promote heat dissipation of birds. The fewer contour feathers in urban great tits may also indicate adaptation to urban heat, but can also be the result of nutritional constraints experienced by urban egg-laying females caused by the altered food availability in cities.

TÉZISPONTOK

A táplálékelérhetőség limitálja a városi madarak szaporodását: kísérlet széncinegéken

1. Vizsgáltam, hogy a városokra jellemző, limitált mennyiségű rovartáplálék hogyan befolyásolja a városi madarak szaporodási sikerét. Kimutattam, hogy azokban a városi fészkekben, amelyben a szülők nem kaptak kiegészítő táplálékot a kísérlet során, a fiókák jelentősen kisebb testmérettel és rosszabb túléléssel jellemezhetők, mint a szintén nem etetett erdei fészekaljak fiókái. Azonban, amikor a városi fészekaljakat kiegészítő táplálékkal láttam el, ezek a különbségek erősen lecsökkentek, és egyes esetekben eltűntek: a fiókák morfológiája és túlélési aránya is elérte vagy nagyon megközelítette az erdei területek kontroll (nem etetett) fészekaljaiban mért értékeket. Az erdei fészkek fiókáira viszont nem volt szignifikáns hatással az kiegészítő táplálék. Eredményeim alapján megállapítható, hogy a városi madarak kisebb testméretéért és alacsonyabb szaporodási sikeréért jelentős részben a táplálék-limitáció a felelős, míg az erdei madarakat szaporodási sikerét jóval kevésbé korlátozza a táplálék elérhetősége.

A városi és az erdei széncinegék tollszerkezeti különbségei: kényszer vagy adaptáció?

2. A városi és erdei széncinegék testtollainak részletes szerkezeti összehasonlítása során kimutattam, hogy a városi környezet csak az elsőéves madarak tollaira van hatással, míg a felnőtt madarak esetében nem találtam kimutatható különbséget. Kimutattam, hogy a városi elsőéves széncinegék testtollai kisebb sűrűségűek, ami végső soron egy lazább tollazatot eredményez. Habár a korábbi vizsgálatok eredményei és értelmezései ellentmondásosak, feltételezhető, hogy a lazább tollazat elősegíti a városi madarak jobb hőleadását, amelynek egyik valószínű mozgatórugója a városi melegebb klímához történő adaptáció.
3. A városi és az erdei széncinegék repülőtollainak (szárny- és faroktollak) összehasonlítása során a felnőtt madarak között semmilyen élőhelyi különbséget nem találtam, azonban az elsőéves madarak esetében a szárnytollak két tulajdonsága is eltérést mutatott a két élőhely között. Korábbi vizsgálatok eredményei alapján feltételezhető, hogy ezek a tulajdonságok negatívan befolyásolják a városi elsőéves madarak repülési képességét, ami végül hatással lehet akár a túlélési esélyeikre is. Az elsőéves madarak szárnytollain megfigyelt különbségek több környezeti hatással is magyarázhatóak, például a városi

környezetre jellemző limitált mennyiségű és minőségű táplálék okozta környezeti kényszerekkel.

Alacsonyabb tollszám a városi széncinege fiókáknál, mint az erdei fajtársaiknál

4. Egy általam kitalált, noninvazív módszer alkalmazásával, városi és erdei élőhelyeken nevelkedő, 6-9 napos széncinege-fiókák tollazati jellemzőit összehasonlítva kimutattam, hogy a városi fiókák kevesebb kontúrtollal rendelkeznek, valamint a tollpásztáik területe is kisebb, ami feltehetőleg nagyobb relatív csupasz testfelületet eredményez. A kevesebb toll jelezheti a városi táplálék-limitáció miatti kényszerek hatásait, ami miatt a madarak kevesebb erőforrást fektetnek a tollazatukba. Ugyanakkor, amennyiben a kevesebb kontúrtoll lazább tollazatot eredményez, a megfigyelt különbség utalhat a városokra jellemző magasabb hőmérséklethez történő adaptációra, melyben a szintén városi fiókáknál megfigyelt, nagyobb csupasz testfelületek is szerepet játszhatnak a hatékonyabb hőleadás révén.

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PUBLICATIONS

Publications and manuscripts included in the thesis

1. Seress, G., **Sándor, K.,** Evans, K.L. & Liker, A. 2020. Food availability limits avian reproduction in the city: An experimental study on great tits *Parus major*. *J. Anim. Ecol.* 89: 1570–1580. DOI: https://doi.org/10.1111/1365-2656.13211
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1. Pipoly, I., Preiszner, B., **Sándor, K**., Sinkovics, Cs., Vincze, E., Seress, G., Bókony, V., Liker, A. (2022) Extreme hot weather has stronger impacts on avian reproduction in forests than in cities. *Frontiers in Ecology and Evolution* 10, 825410. DOI: https://doi.org/10.3389/fevo.2022.825410
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1. **Sándor, K.,** Liker, A., Sinkovics, Cs., Péter, Á., Seress, G. 2019. Effects of urbanization on feather number of great tit *(Parus major)* nestlings. Poszter. 12th European Ornithologists' Union Congress, 2019. 08. 26 – 30, Cluj Napoca, Romania.
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APPENDICES

A/I Supplementary Material to ***Chapter IV***

Table S.IV.1. *Mean ± SE* values of great tits' breeding success in the groups of different habitat × treatment combinations in 2017 (present study), calculated from raw data. Nestling body size traits and nestling numbers were recorded at day 15 post-hatch (hatching day of the first egg = day 1), survival rate between days 3 and 15, and nestling provisioning rate (feeding/nestling/hour) when chicks were 3-5 and 9-11 day old (see main text for more details). Forest site: Vilma-puszta, urban site: Veszprém.

Habitat - treatment combinations	control (forest)	supplemented (forest)	control (urban)	supplemented (urban)
Clutch size[1]	9.67 ± 0.28	10.08 ± 0.29	9.00 ± 0.30	9.00 ± 0.35
Nestling body mass (g)[2]	17.02 ± 0.19	17.85 ± 0.10	14.21 ± 0.25	16.27 ± 0.16
Nestling wing length (mm)[2]	47.61 ± 0.65	48.59 ± 0.28	39.44 ± 0.81	44.53 ± 0.42
Nestling tarsus length (mm)[2]	19.49 ± 0.12	19.83 ± 0.06	18.32 ± 0.17	19.38 ± 0.10
Nestling number (day 15)[2]	8.25 ± 0.51	9.46 ± 0.43	4.50 ± 0.76	6.86 ± 0.44
Nestling survival rate[2]	0.96 ± 0.02	1.00 ± 0.00	0.56 ± 0.09	0.89 ± 0.04
Nestling provisioning rate[3]	4.39 ± 0.67	5.40 ± 0.99	3.81 ± 0.61	5.52 ± 0.85

[1] Number of clutches: forest control / supplemented: 12 / 12, urban control / supplemented: 12 / 15.
[2] Number of broods: forest control / supplemented: 12 / 11, urban control / supplemented: 10 / 14.
[3] Number of broods: forest control / supplemented: 11 / 10, urban control / supplemented: 8 / 13.

Table S.IV.2. *Mean ± SE* values of great tits' breeding success between 2013 and 2016 (nestling body mass and number were recorded at day 14-16; data obtained from Seress *et al.* 2018). Number of broods (forest / urban): 2013: 7 / 29; 2014: 24 / 34; 2015: 21 / 42; 2016: 19 / 44. Forest site: Vilma-puszta, urban site: Veszprém; only first seasonal breeding attempts were used.

		2013	2014	2015	2016
Clutch size	forest	11.86 ± 0.59	11.96 ± 0.27	10.95 ± 0.32	11.5 ± 0.24
	urban	8.97 ± 0.26	11.06 ± 0.3	8.00 ± 0.26	7.98 ± 0.26
Nestling body mass (g)	forest	17.6 ± 0.14	18.0 ± 0.05	17.6 ± 0.09	17.6 ± 0.07
	urban	14.5 ± 0.17	16.2 ± 0.11	14.9 ± 0.14	14.6 ± 0.14
Nestling number	forest	10.43 ± 0.64	9.07 ± 0.45	10.11 ± 0.39	10.31 ± 0.73
	urban	7.22 ± 0.42	10.46 ± 0.55	6.09 ± 0.39	5.36 ± 0.42

Figure S.IV.1. Differences in caterpillar biomass (log_{10}[mg/h]) between the urban (Veszprém - gray) and forest (Vilma-puszta - green) study sites in 2014-2017. Caterpillar biomass was estimated from frass samples collected throughout birds' brood-rearing period (defined for each site and year as from the hatching date of the first brood until the date at which the last of the first broods was 15 d old). For frass sampling, we identified the most common tree species in each study site and sampled six mature tree individuals per species. The selected, dominant tree species were: silver lime *Tilia argentea*, Norway maple *Acer platanoides* and horse-chestnut *Aesculus hippocastanum* at the urban, and flowering ash *Fraxinus ornus* and downy oak *Quercus cerris* at the forest site (see Seress *et al. (*2018) for further details). To compare caterpillar biomass between the two study sites, we fitted LME models separately for each year, in which habitat type (urban or forest) was the predictor and tree species nested in tree ID were random factors. Caterpillar abundance was significantly higher in the forest site in each year (difference in 2014: 7.6-fold, in 2015: 28-fold, in 2016: 36.4-fold, in 2017: 8-fold; $p < 0.004$ in all cases). Data of 2014-2016 was obtained from Seress *et al.* (2018), see it for further methodological details. On the graph medians and interquartile ranges are respectively indicated by the thick middle lines and the boxes, while the whiskers extend to the most extreme data points within 1.5 × interquartile range from the box, and the open circles refer to the outliers.

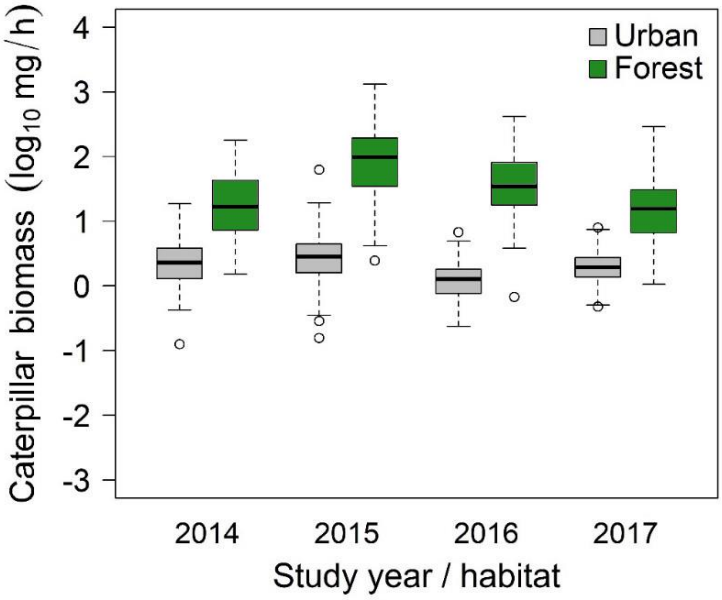


Table S.IV.3. Information on great tit parents' age that were involved in the video analyses (n = 42 broods). Colour ringed individuals were ringed either during winter or in previous breeding seasons. First-year birds hatched in 2016 (i.e. the year before the experiment). Note that the number of ringed birds is somewhat higher in this table (n = 68) than that is reported in the main text (n = 66) because a few individuals were captured, ringed and aged right after the experiment.

Age in 2017	**supplemented (urban)**	**control (urban)**	**supplemented (forest)**	**control (forest)**	**Sum**
non-ringed (unknown age)	3	2	6	5	16
1st year birds	5	0	5	7	17
older birds	18	14	9	10	51
all birds	**26**	**16**	**20**	**22**	**84**
% of 1st-year birds (of known age birds)	21.7% (5/23)	0% (0/14)	35.7% (5/14)	41.1% (7/17)	--
% of 1st-year birds (of all birds)	19.2% (5/26)	0% (0/16)	25.0% (5/20)	31.9% (7/22)	--
% of older birds (of known age birds)	78.3% (18/23)	100% (14/14)	64.3% (9/14)	58.8% (10/17)	--
% of older birds (of all birds)	69.2% (18/26)	87.5% (14/16)	45.0% (9/20)	45.5% (10/22)	--

Table S.IV.4. Initial (full) models (LME for a-d, and GLM for e) of the effects of supplementary feeding and habitat on (a) great tit parents' provisioning rate (log-transformed using the formula $\log_e(x+0.5)$), and their nestlings' (b-d) body size and (e) proportion of survived nestlings (on a logit scale). Statistically significant ($p < 0.05$) differences are highlighted in bold and marginally non-significant ($0.05 < p < 0.10$) differences are shown in italic.

Model parameters	*b ± SE*	*t or z*	*p*
(a) Provisioning rate (feeding/nestling/hour) [1]			
Intercept	1.26 ± 0.42	3.02	0.005
Habitat	-0.26 ± 0.26	-0.98	0.334
Treatment	0.09 ± 0.19	0.48	0.632
Date	0.02 ± 0.03	0.91	0.372
Time of day	-0.00 ± 0.00	-0.33	0.740
Nestling age (9-11 days)	**0.52 ± 0.21**	**2.53**	**0.019**
Habitat × treatment	0.24 ± 0.29	0.83	0.411
(b) Nestling body mass (g; day 15) [2]			
Intercept	16.19 ± 1.51	10.71	<0.001
Habitat	-2.79 ± 0.66	-4.23	<0.001
Treatment	0.79 ± 0.51	1.57	0.125
Date	0.07 ± 0.07	0.99	0.328
Brood size	0.00 ± 0.00	1.30	0.201
Time of day	-0.05 ± 0.12	-0.41	0.682
Habitat × treatment	0.97 ± 0.73	1.33	0.191
(c) Nestling wing length (mm; day 15) [2]			
Intercept	46.95 ± 3.55	13.22	<0.001
Habitat	-8.56 ± 2.17	-3.95	<0.001
Treatment	0.71 ± 1.75	0.40	0.690
Date	0.28 ± 0.25	1.15	0.225
Brood size	0.11 ± 0.41	0.27	0.788
Habitat × treatment	*4.44 ± 2.43*	*1.83*	*0.074*
(d) Nestling tarsus length (mm; day 15) [2]			
Intercept	19.38 ± 0.68	28.62	<0.001
Habitat	-1.20 ± 0.42	-2.88	0.006
Treatment	0.32 ± 0.32	0.99	0.328
Date	**0.09 ± 0.05**	**2.09**	**0.043**
Brood size	0.02 ± 0.08	0.21	0.832
Habitat × treatment	0.71 ± 0.46	1.53	0.134
(e) Nestling survival (between day 3-15) [3]			
Intercept	3.59 ± 1.09	3.28	<0.001
Habitat	-2.69 ± 0.50	-5.36	<0.001
Treatment	2.52 ± 1.48	1.70	0.088
Date	**0.21 ± 0.07**	**3.02**	**0.002**
Brood size	-0.07 ± 0.11	-0.62	0.537
Habitat × treatment	-0.87 ± 1.52	-0.57	0.571

[1] Number of broods: forest control / supplemented: 11 / 10, urban control / supplemented: 8 / 13.

[2] Number of nestlings (number of broods): forest control / supplemented: 99 (12) / 104 (11), urban control / supplemented: 45 (9) / 96 (14).

[3] Number of broods: forest control / supplemented: 12 / 11, urban control / supplemented: 10 / 14.

A/I.1. Coldspell

Figure S.IV.2. *Mean* ± *SE* of daily mean temperatures in April (2014-2017; day 1 = 1st of April) for (a) the urban (Veszprém) and (b) the forest (Vilma-puszta) study sites. The cold spell, i.e. the unusual and sudden drop of temperature, lasted for *c*. 4 days (April 18-21) in both study sites. Data was recorded by a temperature data logger (Voltcraft DL-101T) at each study site.

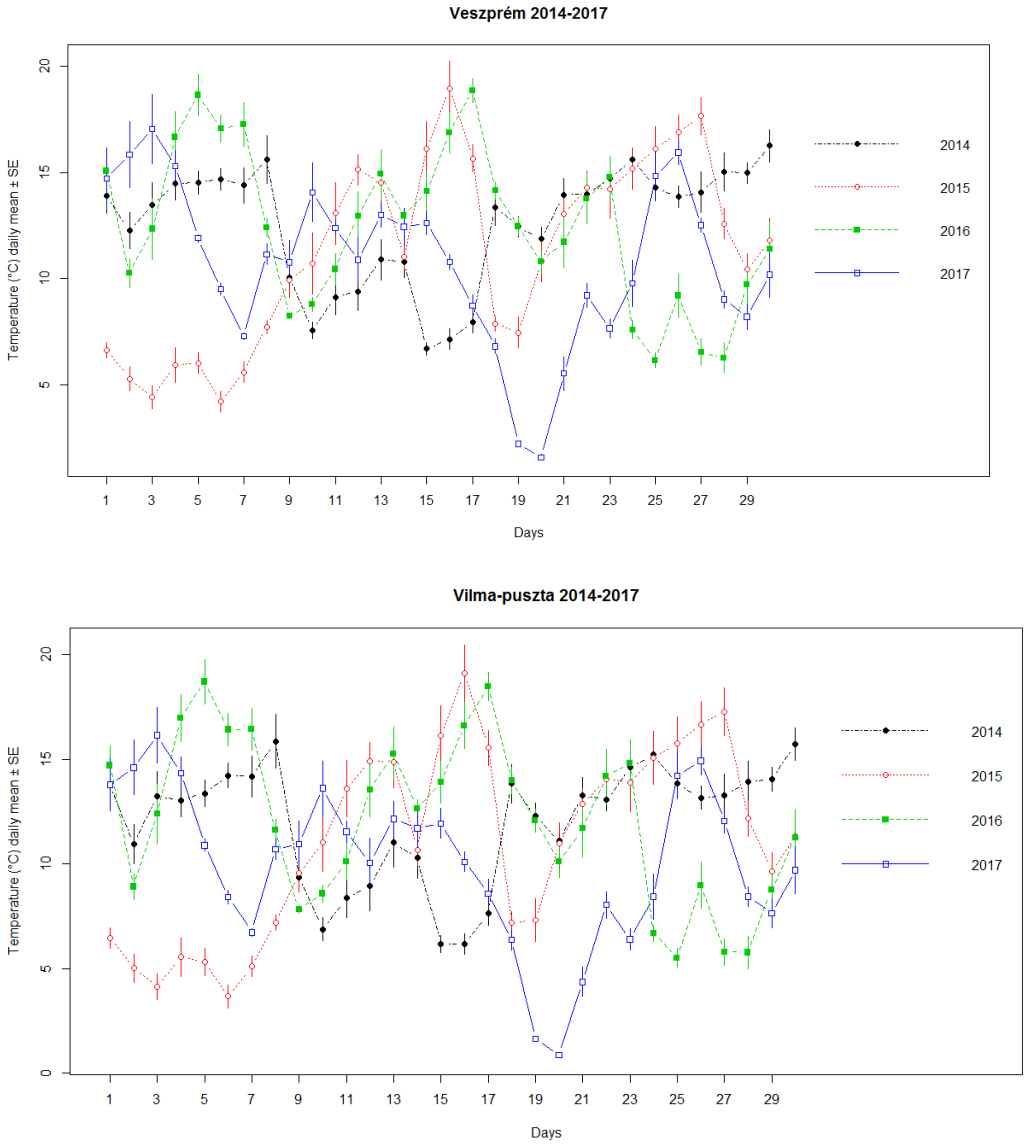


Table S.IV.5. The distribution of broods that were either exposed (already contained chicks) or not exposed (did not contain hatched chicks, i.e. were still incubated) to the cold spell (April 18-21 of 2017) during the nestling phase, in the groups of different habitat × treatment combinations.

Habitat × treatment combinations	**control (forest)**	**supplemented (forest)**	**control (urban)**	**supplemented (urban)**
Exposed to cold spell (nr. of broods)	0	0	8	11
Not exposed to cold spell (nr. of broods)	12	11	2	3

Table S.IV.6. Due to their seasonally earlier egg laying, only urban nestlings were exposed to the 4-day long cold spell, as all the involved forest clutches were still in the incubation phase that time and none of them suffered brood failure in this period (Table S.IV.1). Therefore we used only urban broods in the following analyses. First, we calculated the number of days of exposure to the cold spell for each brood (range: 0-4; *mean* ± *SE*, urban control group: 2.6 ± 0.5, supplemented group: 2.6 ± 0.4 days). Then we fitted separate linear models for broods' mean body mass, mean wing length, mean tarsus length (measured at day 15 post-hatch; hatching day of the first egg = day 1) and survival rate (proportion of nestlings surviving between day 3 and 15), and tested the effect of cold spell exposure treatment (supplemented or control); additional predictors were brood size, and in case of body mass model, the time of day. We used binomial error distribution, logit link function in the survival rate model. The results of initial (full) models are shown below, for sample sizes see Table S.IV.1.

Model parameters	*b* ± *SE*	*t or z*	*p*
(a) Nestling body mass (g; day 15)			
Intercept	12.87 ± 1.76	7.34	<0.001
Treatment	1.81 ± 0.83	2.18	0.044
Cold spell exposure	-0.04 ± 0.25	-0.17	0.867
Brood size	0.04 ± 0.14	0.25	0.805
Time of day	0.00 ± 0.00	1.02	0.324
Cold spell exposure × treatment	-0.03 ± 0.29	-0.09	0.924
(b) Nestling wing length (mm; day 15)			
Intercept	37.98 ± 4.50	8.44	<0.001
Treatment	4.91 ± 3.11	1.58	0.132
Cold spell exposure	-0.61 ± 0.79	-0.77	0.450
Brood size	0.28 ± 0.52	0.53	0.601
Cold spell exposure × treatment	0.31 ± 1.03	0.31	0.763
(c) Nestling tarsus length (mm; day 15)			
Intercept	18.51 ± 0.92	2.20	<0.001
Treatment	1.09 ± 0.64	1.71	0.104
Cold spell exposure	-0.21 ± 0.16	-1.29	0.213
Brood size	0.02 ± 0.11	0.22	0.832
Cold spell exposure × treatment	0.03 ± 0.21	0.16	0.872
(d) Nestling survival (between days 3-15)			
Intercept	0.86 ± 1.05	0.82	0.413
Treatment	2.87 ± 1.02	2.82	0.005
Cold spell exposure	-0.10 ± 0.16	-0.60	0.549
Brood size	-0.05 ± 0.12	-0.36	0.716
Cold spell exposure × treatment	-0.36 ± 0.30	-1.20	0.231

Table S.IV.7. Comparison of mean nestling body mass of urban control broods that were exposed to the cold spell during the nestling phase (2017, present study) to mean nestling body mass of urban broods from 2013-2016 (from the same urban site) that did not experience such weather during the nestling phase. We included only non-manipulated broods where nestlings were measured at day 15 post-hatch (hatching day of the first egg = day 1). Results are from linear model, statistically significant ($p < 0.05$) differences are highlighted in bold. Nestling body mass was not significantly different between years – the only exception is 2014 when monthly mean temperatures were unusually warm in February-March (see Seress *et al.* 2018 Appendix S1). Nr. of broods: 2013: 18; 2014: 13; 2015: 18; 2016: 14; 2017: 8.

Model parameters	*b* ± *SE*	*t*	*p*
Nestling body mass (g; day 15)			
Intercept (Year 2017)	14.09 ± 0.63	22.26	<0.001
Year 2013	0.72 ± 0.75	0.97	0.337
Year 2014	**1.98 ± 0.79**	**2.52**	**0.014**
Year 2015	0.90 ± 0.75	1.21	0.231
Year 2016	0.18 ± 0.78	0.23	0.816

Table S. V.I. The results of the final linear model of contour feathers traits. These final models were used for calculating linear contrast of habitat differences (see Table V.1 in ***Chapter V***). The model contained the study site as the main effect (four levels), sex, age (FY or AFY), and year of moult as predictors, and the site × age interaction. Statistically significant results ($p < 0.05$) are indicated by bold, marginally non-significant results are ($0.05 < p < 0.1$) are indicated by italic.

	Contour feathers			
	Sum of Sq	*df*	*F*	*p-value*
Pennaceous density (barbs/mm)				
Site	0.65	3	2.91	**0.035**
Sex	0.05	1	0.66	0.416
Age	0	1	0	0.975
Year of moult	0	1	0	0.967
Site × age	0.84	3	3.72	**0.012**
Plumulaceous density (barbs/mm)				
Site	0.48	3	2.21	0.088
Sex	0.16	1	2.25	0.135
Age	0.44	1	6.04	**0.014**
Year of moult	0.26	1	3.67	0.056
Site × age	0.21	3	0.96	0.412
Pennaceous length (mm)				
Site	4.88	3	1.7	0.168
Sex	14.05	1	14.67	**< 0.001**
Age	2.66	1	2.78	0.096
Year of moult	9.28	1	9.69	**0.002**
Site × age	8.26	3	2.87	**0.037**
Plumulaceous length (mm)				
Site	23.27	3	5.93	**< 0.001**
Sex	0	1	0	0.960
Age	0	1	0	0.979
Year of moult	2.87	1	2.19	0.140
Site × age	1.09	3	0.28	0.841
Total number of pennaceous barbs				
Site	3.14	3	0.28	0.843
Sex	46.83	1	12.34	**< 0.001**
Age	13.65	1	3.60	0.059
Year of moult	58.63	1	15.44	**< 0.001**
Site × age	6.76	3	0.59	0.619
Total number of plumulaceous barbs				
Site	104.16	3	5.61	**0.001**
Sex	14.85	1	2.40	0.123
Age	30.02	1	4.85	**0.029**
Year of moult	0.83	1	0.13	0.714
Site × age	14.45	3	0.78	0.507

Table S.V.2. The results of the final linear models for (a) wing and (b) tail feather traits. These final models were used for calculating linear contrasts of habitat differences (see Table V.2 in ***Chapter V***). The models contained the study site (four levels), sex, age (FY or AFY), and year of moult as predictors, and the site × age interaction. Statistically significant results ($p < 0.05$) are indicated by bold, marginally non-significant results are ($0.05 < p < 0.1$) are indicated by italic.

	(a) Wing feathers				(b) Tail feathers			
	Sum of Sq	*df*	*F*	*p-value*	*Sum of Sq*	*df*	*F*	*p-value*
Feather length (mm)								
Site	7.65	3	1.24	0.296	0.90	3	0.10	0.959
Sex	158.99	1	77.33	< **0.001**	481.09	1	161.61	< **0.001**
Age	35.92	1	17.47	< **0.001**	26.56	1	8.92	**0.003**
Year of moult	5.62	1	2.73	0.099	1.59	1	0.53	0.466
Site × age	2.11	3	0.34	0.794	9.12	3	1.02	0.384
Rachis width (mm)								
Site	0.01	3	2.53	*0.058*	0	3	0.94	0.424
Sex	0.05	1	30.73	< **0.001**	0.07	1	38.44	< **0.001**
Age	0.05	1	31.63	< **0.001**	0	1	0	0.991
Year of moult	0	1	0	0.983	0.02	1	10.91	**0.001**
Site × age	0.02	3	4.86	**0.002**	0.02	3	2.96	**0.033**
Barb density (nr. of barbs/cm)								
Site	2.20	3	0.22	0.881	9.50	3	2.04	0.11
Sex	1.61	1	0.49	0.485	0.39	1	0.25	0.617
Age	17.43	1	5.27	**0.022**	0.20	1	0.13	0.717
Year of moult	17.84	1	5.39	**0.021**	39.49	1	25.39	< **0.001**
Site × age	7.28	3	0.73	0.533	2.83	3	0.61	0.611
Barbule density (nr. of barbules/mm)								
Site	33.22	3	3.73	**0.012**	15.72	3	1.25	0.291
Sex	1.53	1	0.51	0.474	6.24	1	1.49	0.223
Age	69.16	1	23.31	< **0.001**	1.08	1	0.26	0.611
Year of moult	8.00	1	2.70	0.102	1.33	1	0.32	0.573
Site × age	25.92	3	2.91	**0.035**	12.56	3	1.00	0.392

Table S.V.3. Differences in the structural properties of the contour feathers between urban and forest great tits were tested separately for first-year (FY) and after first year (AFY) birds. Linear contrasts comparing the two habitat types within the age groups were calculated from linear models presented in Table S.V.1. Positive values indicate higher values in urban birds. Statistically significant ($p < 0.05$) differences are highlighted in bold.

	Contour feathers			
	contrast ± SE	*df*	*t ratio*	*p-value*
Pennaceous density (barbs/mm)				
FY	-0.11 ± 0.05	199	-2.27	**0.024**
AFY	0.01 ± 0.07	199	0.11	0.909
Plumulaceous density (barbs/mm)				
FY	-0.13 ± 0.05	198	-2.58	**0.010**
AFY	-0.02 ± 0.07	198	-0.29	0.77
Pennaceous length (mm)				
FY	0.36 ± 0.18	199	2.02	**0.045**
AFY	-0.31 ± 0.26	199	-1.17	0.244
Plumulaceous length (mm)				
FY	0.61 ± 0.21	199	2.91	**0.004**
AFY	0.39 ± 0.31	199	1.29	0.199
Total number of pennaceous barbs				
FY	0.10 ± 0.36	199	0.29	0.770
AFY	-0.67 ± 0.52	199	-1.29	0.199
Total number of plumulaceous barbs				
FY	0.89 ± 0.46	198	1.95	*0.052*
AFY	1.19 ± 0.67	198	1.78	0.076

Table S.V.4. Differences between urban and forest first-year (FY) and after first year (AFY) great tits in the structure of (a) wing and (b) tail feathers. Linear contrasts comparing the two habitat types within the age groups were calculated from the linear models presented in Table S.V.2. Positive values indicate higher values in urban birds.

	(a) Wing feathers				(b) Tail feathers			
	contrast ± SE	*df*	*t ratio*	*p-value*	*contrast ± SE*	*df*	*t ratio*	*p-value*
Feather length (mm)								
FY	-0.15 ± 0.27	187	-0.57	0.570	-0.16 ± 0.34	173	-0.46	0.648
AFY	-0.31 ± 0.39	187	-0.8	0.426	-0.07 ± 0.48	173	-0.15	0.879
Rachis width (mm)								
FY	-0.02 ± 0.01	187	-3.13	**0.002**	0 ± 0.01	177	0.31	0.760
AFY	0.02 ± 0.01	187	1.58	0.116	0.01 ± 0.01	177	0.86	0.388
Barb density (barbs/cm)								
FY	0.18 ± 0.34	185	0.51	0.612	-0.15 ± 0.24	175	-0.62	0.533
AFY	0.43 ± 0.49	185	0.86	0.389	0.24 ± 0.35	175	0.71	0.479
Barbule density (barbules/mm)								
FY	0.84 ± 0.32	187	2.60	**0.010**	0.53 ± 0.4	177	1.34	0.181
AFY	-0.80 ± 0.47	187	-1.70	0.090	-0.58 ± 0.56	177	-1.03	0.303

Table S.V.5. To test whether feather abrasion affected the length of the pennaceous part of the contour feathers (that are usually the most exposed to abrasion) we run an additional analysis that includes capture season (summer versus winter, see ***Chapter V,*** section *5.2. Methods*) in the linear model (a). Furthermore, we repeated the calculation of linear contrasts using estimates from this model (b). Note that although the estimations of the linear contrasts have changed slightly, the main conclusions of habitat comparisons remained unaffected, i.e. these indicate a significant habitat difference in pennaceous length in FY but not in AFY birds.

(a) LM model					(b) Linear contrasts				
	Sum of Sq	*df*	*F*	*p-value*		*contrast ± SE*	*df*	*t ratio*	*p-value*
Site	7.11	3	2.52	0.059	FY	0.45 ± 0.18	198	2.47	**0.014**
Sex	11.35	1	12.06	**0.001**	AFY	-0.14 ± 0.27	198	-0.51	0.608
Age	1.28	1	1.36	0.244					
Year of moult	10.36	1	11.01	**0.001**					
Season [1]	4.36	1	4.64	**0.032**					
Site × age	6.55	3	2.32	0.077					

[1] Number of birds (forest/urban) captured during the breeding season: 70/90 and winter: 45/6.

Table S.V.6. The results of intraclass correlation analyses showing the within-observer repeatability of the measured variables. We tested repeatability by repeating the measurements for randomly selected 20 wing feathers and 20 contour feathers. Because in the case of wing and tail feathers we measured exactly the same variables with the same methodology and microscope settings we tested repeatability only on wing feathers. KS performed all measurements, and the statistical analyses were conducted by using the ICC function of the *'irr'* R package.

Measured variable	Intraclass correlation			
	ICC	*95% confidence interval of ICC*	*F*	*p-value*
		Flight feathers		
Feather length	0.972	0.933-0.989	10.2	< **0.001**
Rachis width	0.897	0.762-0.958	2.63	**0.019**
Nr. of barbs	0.881	0.728-0.951	2.24	**0.039**
Nr. of barbules	0.89	0.747-0.955	2.45	**0.027**
		Contour feathers		
Pennaceous length (mm)	0.997	0.993-0.999	107	< **0.001**
Plumulaceous length	0.999	0.998-1	387	< **0.001**
Nr. of pennaceous barbs	0.963	0.911-0.985	7.57	< **0.001**
Nr. of plumulaceous barbs	0.986	0.965-0.994	19.7	< **0.001**

A/III Supplementary Material to ***Chapter VI***

A/III.1. Temperature

From 2013 we continuously collected hourly temperature data at each study site with a Voltcraft DL-101T temperature and humidity data logger (Conrad Electronic SE, Germany; one data logger per site). We calculated daily mean temperatures (involving all months during the year) for the period 2013-2018. To test temperature differences between habitats (n = 4016 forest, n = 4025 urban daily mean temperature records), first, we fitted an LME model (*'nlme'* package) for daily mean temperatures, including sites (four levels) and years (six levels) as factors, and month as a random factor. Then, we calculated linear contrasts between the two habitat groups, using *'emmeans'* function (package *'emmeans'*) as described in the main text. Although years significantly differed in daily mean temperature ($\chi_{2(1)} = 5.470$, $p < 0.0193$), the linear contrast showed significantly lower temperatures at our forest compared to urban habitats (forest compared to urban: $contrast \pm SE = -1.83 \pm 0.1$, $t = -20.77$, $p < 0.001$, Figure S.VI.1a).

A/III.2. Food availability

Between 2013 and 2016 we also conducted caterpillar abundance measurements in our study sites. To do so, we applied a commonly used frassfall (caterpillar dropping) sampling method (Tinbergen & Dietz 1994) during each years' avian breeding season (between March and June) and estimated caterpillar biomass from frass samples (for more details see Seress *et al.* 2018). We transformed caterpillar biomass (mg/h) as $\log_{10}(x + 0.0001)$, and we used it as a dependent variable in the LME model. The model contained site (four levels) and years (four levels) as factors, and we used tree species nested in tree ID as random factors (for more details see Seress et al. 2018). Then, we calculated linear contrasts between the two habitat groups, using *'emmeans'* function (package *'emmeans'*) as described in the main text. The results of the linear contrast showed significantly higher caterpillar biomass in the forest habitat type (forest compared to urban: $contrast \pm SE = 0.55 \pm 0.1$, $t = 7.5$, $p = 0.001$, Figure S.VI.1b). When analysed separately for each year, Seress *et al.* (2018) also showed that this habitat difference was consistent over each study year, showing 2.6-12.5-fold higher caterpillar biomass at forest compared to urban sites.

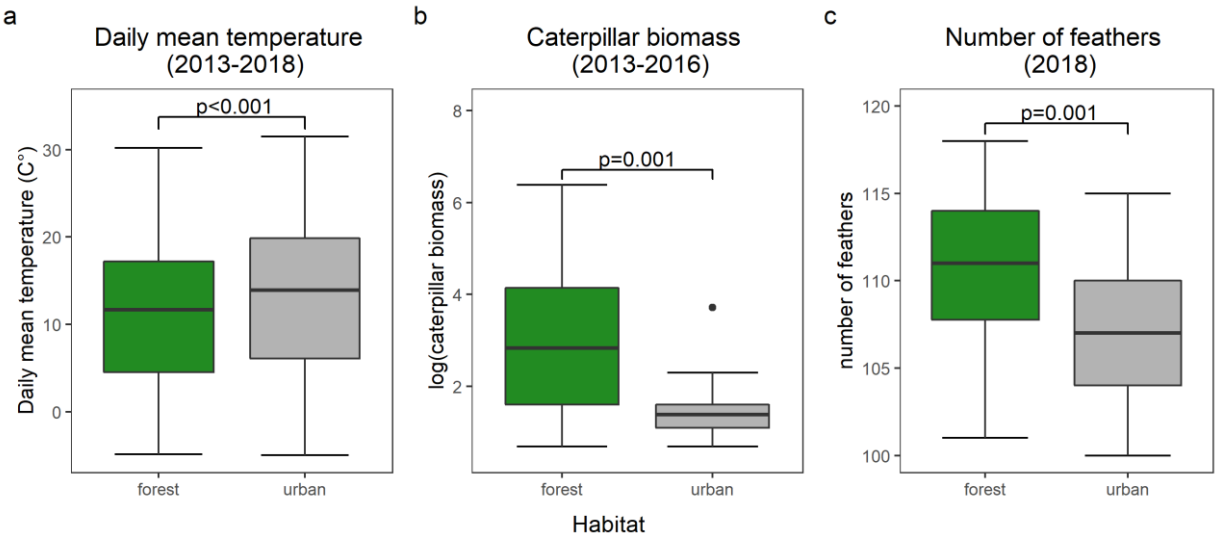


Figure S.VI.1. Habitat differences in the daily mean temperatures (a), caterpillar biomass (log_{10}[mg/h]) (b), and the number of feathers (c) between urban and forest habitats in our study system. The significantly lower number of feathers in urban great tit nestlings may be due to an adaptation to the warmer urban climate, or result from environmental constraint due to the low availability of caterpillars (the optimal food source for great tit nestlings) in urban habitats. Medians, interquartile ranges and data ranges are shown by the middle thick lines, the boxes, and the whiskers, respectively.

A/III.3. Feather measurements

During the data extraction from the photographs, we excluded the data of 42 nestlings (30 urban and 12 forest chicks), either due to poor image quality or because the sampled nestlings' feather sheaths were already brush-like open (thus partially overlapping occasionally), hampering the precise counting of individual feathers within the feather tract.

We tested the reliability of our measurements two ways. For the two main variables (feather number, feather density), and also to the area of the examined feather tract two independent observers (KS and Anudari Batsaikhan) performed measurements on each photo, and for within-observer repeatability we randomly selected 40 photos that were measured twice by KS (with ca. 2 weeks between the repeated measurements). The between- and within-measurer repeatability was tested by intraclass correlation (function '*ICC'*, from R package *'irr'*). The repeatability was high for all variables both between obserwers (feather number: *ICC* = 0.825, 95% *CI:* 0.77-0.87, *F* = 1.49; feather density: *ICC* = 0.976, *CI* 0.97-0.98, *F* = 11.8; area: *ICC* = 0.982, *CI* 0.98-0.99, *F* = 15.8; *n* = 171, all $p < 0.001$) and within-observer (feather number: *ICC* = 0.935, 95%, *CI* 0.88-0.96, *F* = 4.28; feather density: *ICC* = 0.99, *CI* 0.98-0.99, *F* = 31.6; area: *ICC* = 0.99, *CI* 0.98-0.99, *F* = 36.2; *n* = 40, all $p < 0.001$).

A/III.4. Nestling fat score

In 2018, we estimated the amount fat reserves of urban and forest great tit nestlings at 14-16 days of age (i.e. a few days prior to fledging). We followed the methods of Biometrics Working Group (BWG) of the British & Irish Ringing Scheme and scored the visible fat in the tracheal pit on a 9-level scale (from 0 to 8; Redfern *et al.* 2001). Note that since we did not individually mark or ring nestlings that were involved in the current study (at 6-9 d age, 2-3 chicks per brood), we decided to use the fat score data of all nestlings belonging to the involved broods (n = 272 forest and n = 250 urban nestlings). For habitat comparison, we fitted cumulative link mixed model (CLMM, function *'clmm'*, package *'ordinal'*) for the nestlings' fat score (dependent variable), and included study site (four levels), body mass, and brood size as predictors, and nest ID as a random factor. Then, we calculated linear contrasts between the two habitat groups (urban vs. forest), using *'emmeans'* function (package *'emmeans'*) as described in the main text. The results of linear contrast showed no significant differences in fat deposits between urban and forest nestlings (*contrast* ± *SE:* 0.41 ± 0.7, z = 0.6, p = 0.561).

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