HABITAT AND SEASONAL DIFFERENCES IN THE DIET OF GREAT TIT *(PARUS MAJOR)* NESTLINGS

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Ph.D. Thesis
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ÉLŐHELYI ÉS SZEZONÁLIS KÜLÖNBSÉGEK SZÉNCINEGE *(PARUS MAJOR)* FIÓKÁK TÁPLÁLÉK-ELLÁTOTTSÁGÁBAN

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Contents

Abstract

Currently over half of the human population lives in cities and the increasing trend of urbanization is expected to continue in the foreseeable future. Transforming natural habitats into urbanized areas poses a challenge for wildlife due to the altered environmental conditions. Thus, understanding the impact of urbanization on ecosystems is urgent to mitigate its adverse effects.

This thesis focuses on a common insectivorous bird, the great tit *(Parus major)* which often suffers from inferior breeding success in urban compared to natural habitats, which is mainly manifested in lower clutch size, lower nestling weight and lower nestling survival in cities. According to the food limitation hypothesis, the amount of high quality insect food (caterpillars) is not sufficient for healthy nestling development in urban habitats, which results in lower reproductive success. The aim of the present thesis was to investigate the habitat and seasonal differences in great tit nestlings' diet to better understand the mechanisms underlying this phenomenon. For this purpose, we made one-hour-long video recordings of the feeding behaviour of nesting great tits in urban and forest habitats to compare the composition and amount of food they provide to their offspring. We conducted a three-year-long study and (i) investigated whether our prey-measuring process from video recordings provided suitable and accurate estimates on quantifying the size of prey items, (ii) compared the composition and amount of nestling food between urban and forest populations during their annual first broods, and also (iii) investigated the seasonal differences in nestling diet between their annual first and second broods within urban and forest habitats.

According to our results, in those years when we observed lower caterpillar biomass and reduced reproductive success in urban compared to forest habitats, urban parents provided less caterpillars and more non-arthropod food items than forest parents, although the amount of food provided to the nestlings did not differ between habitats. However, in one special year when we observed only small habitat differences in both caterpillar biomass and the birds' reproductive success, urban parents were able to provide more arthropods and almost twice as large caterpillars to their offspring compared to the other years. We also showed that regarding second broods, forest parents were able to adjust their brood size properly to the seasonal decline of caterpillar availability, since they were able to feed their nestlings with similar quality and amount of food resulting in similar nestling body mass and survival in first and second broods. In contrast, in urban second broods parents tended to deliver fewer caterpillars and the nestlings had lower survival than in first broods, which suggests that brood-size adjustment in this habitat is insufficient to compensate for the reduced food quality available for second broods. The results presented in this thesis supported the food limitation hypothesis in urban habitat, i.e. the availability of caterpillars is probably the major driver of the reduced reproductive success of the great tits in the studied cities.

Kivonat

Jeleleg az emberiség több, mint fele városokban él és az urbanizáció mértéke a belátható jövőben is folytatódni fog. A természetes élőhelyek városokká alakítása a vadon élő állatok számára jelentős kihívást jelent a megváltozott környezeti feltételek miatt, ezért az urbanizáció ökoszisztémákra gyakorolt hatásának megértése elengedhetetlen ahhoz, hogy a káros következményeket mérsékelhessük.

Az alábbi doktori tanulmány az egyik leggyakoribb rovarevő madarunkra, a széncinegére *(Parus major)* fókuszál, amely városokban gyakran gyengébb költési sikert ér el, mint természetes élőhelyeken, ami főképp a kisebb fészekaljméretben, a fiókák alacsonyabb tömegében és alacsonyabb túlélésében nyilvánul meg. A táplálékimitációs hipotézis szerint a városi élőhelyen a fiókák megfelelő fejlődéséhez szükséges jó minőségű rovartáplálék (hernyók) mennyisége nem elegendő, ami a szaporodási siker csökkenését eredményezi. Jelen tanulmány célja megvizsgálni a széncinege-fiókák táplálékának élőhelyi és szezonális különbségeit, hogy jobban megértsük a jelenség hátterében álló mechanizmusokat. Ebből a célból egyórás videófelvételeket készítettünk városi és erdei élőhelyeken fészkelő széncinegék fióka-etetési viselkedéséről, hogy összehasonlíthassuk, milyen összetételű és mennyiségű táplálékot adnak fiókáiknak. A három évig tartó vizsgálat során (i) meghatároztuk, hogy a videofelvételeken végzett méréseink megfelelő és pontos becsléseket adnak-e a hordott zsákmány méretéről, (ii) összehasonlítottuk a fiókák táplálékának összetételét és mennyiségét városi és erdei populációkban, valamint (iii) megvizsgáltuk a fiókák táplálékának szezonális változásait városi és erdei élőhelyeken belül.

Eredményeink szerint azokban az években, amikor a városi élőhelyeken alacsonyabb hernyóbiomasszát és csökkent szaporodási sikert tapasztaltunk az erdei élőhelyekhez képest, a széncinege szülők kevesebb hernyót és több nem-ízeltlábú táplálékot hordtak fiókáiknak, mint az erdeiek, noha a táplálék mennyisége nem különbözött az élőhelyek között. Azonban abban a kivételes évben, amikor a városi és erdei élőhelyeken kisebb mértékű különbséget észleltünk mind a hernyóbiomasszában, mind pedig a széncinegék szaporodási sikerében, a városi széncinegék több ízeltlábúval és közel kétszer akkora hernyókkal etették fiókáikat a többi évekhez képest. Továbbá azt is kimutattuk, hogy az erdei széncinegék a másodköltések során megfelelően tudták igazítani fészekaljméretüket a hernyók mennyiségének szezonális csökkenéséhez, mivel hasonló összetételű és mennyiségű táplálékkal tudták etetni a két fészekalj fiókáit. Az első költéshez hasonló étrend a másodköltéses erdei fiókák magas testtömegét és túlélését eredményezte. Ezzel szemben a városi szülők hajlamosak voltak kevesebb hernyót szállítani másodköltéses fiókáiknak, és a másodköltések fiókáinak túlélése is elmaradt az első költésekhez képest. Ezek az eredények arra utalnak, hogy a városi széncinegék nem képesek megfelelően igazítani fészekaljméretüket a hernyómennyiség szezonális csökkenéséhez. Összegezve, a jelen tanulmányban közölt eredmények alátámasztják a táplálékimitációs hipotézist, vagyis a vizsgált városokban valószínűleg a csökkent hernyómennyiség a fő hajtóereje a széncinegéknél megfigyelhető csökkent szaporodási sikernek.

CHAPTER I

General introduction

1.1. Cities as a novel habitats for wildlife and their impact on animals' reproduction

The process of urbanization includes both the growth of urban human population and the expansion of urban land areas. Approximately half of all humanity lives in cities today, and according to the latest forecasts it will likely increase up to 70 % by 2050 (United Nations, Report 2022/11). The conversion of Earth's land surface to urban use is one of the most irreversible human impacts on the biosphere. Urban settlements differ from natural habitats in numerous ways. Cities are characterized by an altered landscape, including reduced, exotic and fragmented vegetation, high density of buildings and impermeable surface coverings, as well as altered climatic conditions ('urban heat island'). The concentrated human activity in urban areas also leads high air, chemical, light, noise and waste pollution which poses a huge challenge to wildlife (Seress and Liker 2015).

As a consequence of the altered habitat, urban environment has numerous ecological effects on organisms from the individual to the community level. Only those species that are able to adapt to this novel set of conditions can survive in cities, hence species composition and richness of urban communities often differ significantly from the surrounding natural habitats (Reis et al. 2012). Although the patterns are by no means universal, the species richness of the urban flora and fauna often decreases with extreme urbanization (Mckinney 2008), as it has been reported for various taxa such as plants (Yan et al. 2019; Ruas et al. 2022), soil invertebrates (Szabó et al. 2023), arthropods (Piano et al. 2020), amphibians (Callaghan et al. 2021), reptiles (French et al. 2018; Cordier et al. 2021) mammals (Fidino et al. 2020) and birds (Batáry et al. 2018). Whereas species richness and diversity become increasingly impoverished with urban development, populations of certain wild species can be found in higher abundances in more urbanized areas, which is probably due to that some generalist species (called 'urban exploiters') can adapt well to the urban environment and achieve high densities (Szabó et al. 2023).

Urbanization also has various effects on the reproduction of animals. First, most human-inhabited areas are polluted to some extent, which may affect the animals' reproductive cycle through altering their biorhythms and health status. One of the most serious problems that affects wildlife invisibly is chemical pollution, i.e. the introduction of harmful synthetic or naturally occurring chemicals into the environment.

These chemicals can come from a variety of sources, such as industrial activities, agriculture, vehicle traffic, waste disposal and so forth. One group of harmful pollutants are those metals (called ’heavy metals’) that are toxic at low quantity, e.g. lead (Pb), cadmium (Cd), mercury (Hg), arsenic (As) and chromium (Cr). They enter nature from various antropogenic sources, e.g. leaded gasoline, plastic, paints, wood preservative, lead plumbing pipes and so forth. They penetrate animals by means of food, drinking contaminated water, respiration of polluted air or absorption through the skin. Compounds containing heavy metals are toxic in themselves, but what makes them especially dangerous is their ability to bioaccumulate in tissues, by which they can reach and destroy animals at higher trophic levels (Yung et al. 2019). Regarding the animals’ reproductive system, chronic exposure to heavy metals can lead to various diseases in nervous system, fetal abnormality, embryotoxicity and some of them act as xenoestrogens, mimicking the function of estrogen (reviewed in Verma et al., 2018). Another chemical pollutant is plastic, which has recently become the focus of scientific interest as its production and usage is rapidly increasing since the 1960s (Gall and Thompson 2015). Although plastic particles are already found in all corners of the world (Jambeck et al. 2015) from the Mariana Trench (Peng et al. 2018) to polar regions (Bessa et al. 2019), their true and various impacts on ecosystems are still little known. It has been recorded that ingesting larger plastic items can cause physical injuries of animals’ internal organs and reduce reproductive capacity (Gil-Delgado et al. 2017). However, it was discovered only in the last few decades that plastic can break down into very small pieces (called ‘micro- and nanoplastic’) that can enter the blood stream (Leslie et al. 2022) and also have the ability to bioaccumulate in tissues (Mohamed Nor et al. 2021). Microplastics can even cross the blood–brain barrier, appear in brain tissues within 2 hours after ingestion (Kopatz et al. 2023), can cause apoptosis (Danopoulos et al. 2022) and can have an adverse effects on the ovaries and thus could be a potential risk factor for female infertility (Hou et al. 2021). Additionally, plastic can release harmful chemicals into the environment, such as endocrine-disrupting chemicals (EDCs), which can mimic or block natural hormones, leading to reproductive disorders including (but not limited to) infertility and abnormal sexual development in animals (Diamanti-Kandarakis et al. 2009). Note that the above mentioned chemical pollutants are only some of the various types of synthetic compounds that can affect the reproduction of wild animals.

Light pollution is another rapidly growing global problem related to urban settlements. ’Ecological light pollution’ refers to the alteration of natural light regimes in terrestrial and aquatic ecosystems. Global light pollution is continuously increasing and urban areas are highly affected by it. A recent study showed that the average night sky got brighter by 9.6% per year from 2011 to 2022 (Kyba et al. 2023) which, as an exponential trend, means doubling the brightness of the sky every 8 years. The brightness of the European continent has overall increased over the last eight years (especially in Eastern Europe), however, some countries show opposite trends (e.g. France, UK and the Northern countries; Widmer et al., 2022). Those species that are active at dusk or at night and those that use light as communication signals are especially affected by the harmful effects of light pollution. The main mechanisms that directly or indirectly lead to changes in reproduction are disruption of the animals' biorhythm, alteration of their hormone production and elicitation of behavioural responses (Longcore and Rich 2004). The impact of artificial night lights on reproductive performance of animals is demonstrated in many taxonomic groups including insects (Elgert et al. 2020; Owens et al. 2020), molluscs (Hussein et al. 2021), turtles (Silva et al. 2017), nocturnal mammals (Shier et al. 2020) and birds (Dominoni et al. 2013; Dominoni 2015).

Another form of anthropogenically driven environmental change in urban habitat is noise pollution, i.e. change in the acoustic environment (Kunc and Schmidt 2019). The major source of urban noise pollution is traffic which is an all-day phenomenon but generally more intense at daytime (especially in the mornings and evenings; Raza et al., 2011). Noise pollution has been recognized as a major problem for terrestrial and aquatic wildlife as it can lead to a wide range of health issues including developmental, physiological and behavioural changes (Kunc et al. 2016; Shannon et al. 2016). A recent meta-analysis on animals found clear evidence that noise affects species of all studied taxonomic groups including amphibians, arthropods, birds, fishes, mammals, and molluscs (Kunc and Schmidt 2019). Elevated noise pollution directly affects animals' reproduction success, for example, it masks the vocal communication between the individuals that are related to territorial defence or mate quality (Habib et al. 2007; McLaughlin and Kunc 2012). It can also induce physiological changes which lead to changes in hormone level system (e.g. testosterone, cortisol; Abtahi-Eivary et al., 2021).

One of the most characteristic features of the urban environment is the altered meteorological conditions compared to the surrounding area (Parlow 2011). The phenomenon called 'urban heat island' (UHI) means higher average temperature in urban environment (Pickett et al. 2011). The reason for this elevated temperature is that urban surfaces are mostly covered by concrete and asphalt which absorb and emit heat to a greater extent than most natural surfaces. This results in urban environments being up to several degrees warmer than natural habitats (Seress and Liker 2015; Pipoly et al. 2022). Moreover, not only the average temperature is higher in urban environments, but also heat waves become more frequent. Temperature data from more than 200 cities between 1973-2012 showed that almost half of them had statistically significant increase in the number of hot days, and more than 60% had an increase in the number of hot nights (Mishra et al. 2015). These altered meteorological conditions can have various impacts on the reproduction of many organisms including arthropods (Zizzari and Ellers 2011; Roitberg and Mangel 2016), reptiles (Dayananda et al. 2017) and birds (Oswald et al. 2021; Pipoly et al. 2022). The effect of temperature depends on its duration and intensity, it can cause metabolic disruptions, oxidative stress, immune suppression and even death (Lacetera 2019). A recent study indicated that heat exposure in young animals is also associated with a shorter telomere length which may lead to a shorter lifespan and reduced fitness (Eastwood et al. 2022).

The expansion of urban areas is one of the most pervasive causes of habitat loss and fragmentation; the latter is defined as the division of natural habitats into smaller, isolated patches. These processes can have significant impacts on the reproduction of animals depending on the specific taxa (Fahrig 2003). Urban green patches are often located far away from each other without ecological corridors (called step-stone habitats). This habitat fragmentation facilitates the isolation of individuals from potential mating partners which can cause genetic variation loss especially in those species that are less motile (Schmidt et al. 2020). For example, a recent study on a common wild bee *(Ceratina calcarata)* in urbanized areas reported lower genetic diversity and elevated levels of inbreeding compared to more natural habitats (Chau et al. 2023). Populations with low genetic diversity may not be able to respond to environmental fluctuations, become less resilient, more prone to local extensions as well as have increased susceptibility to genetic disorders (Lacy 1997; Hughes et al. 2008). Habitat fragmentation also creates relatively more habitat edges, i.e. where different habitat types meet. Edge areas can be found on the verge of the cities where the local natural vegetation meets the built environment, but also where an urban green area such as a park meets the surrounding buildings. These edges often have distinct environmental conditions, degree of pollution, species composition and ecological dynamics compared to the interior of the habitat patches (called ’edge effect’, Ries et al. 2004). For instance, a study conducted in Tokyo found significant decrease in carabid beetles’ species richness and abundance in edge areas compared to the core zones (Soga et al. 2013). The edge areas may also alter predator-prey dynamics as shown in birds where increased nest predation risk was detected (Batáry and Báldi 2004). Since plants provide essential trophic resources such as food, shelter, cover, breeding sites etc., the composition and type of vegetation basically determines the occurrence, abundance and reproductive output of wild animals. An over a decade-long experimental study demonstrated that even small losses of plant biodiversity may cause considerable long-term losses of wildlife throughout the food web (Haddad et al. 2009). In urban areas the composition and diversity of flora usually differs from the local natural areas due to two main reasons. First, the aforementioned environmental causes such as pollution, the degree of fragmentation and altered microclimate conditions determinate the composition of urban flora, i.e. which species can spread which areas. Second, city park managers often prefer to plant introduced and even invasive plant species, due to their supposed greater resilience in the altered environmental conditions of urban habitats (Sjöman et al. 2016), which species often outcompete native flora for space, light and nutrients (Hejda et al. 2009). Furthermore, there is a new tendency in large cities to replace natural grass with artificial grass (made of synthetic compounds) which do not support urban ecosystems at all (Bernat-Ponce et al. 2020). Beside the altered species composition, vegetation in urban parks is often subject to more intensive treatment such as mowing and the use of various pesticides which have detrimental effect on wildlife from individual to population level (Köhler and Triebskorn 2013). Although the specific pesticides used in urban parks depend on management practices, local regulations and pest control needs, there are some common types of pesticides that are often used in urban park settings (Md Meftaul et al. 2020). Glyphosate is one of the most widespread pesticides used in agriculture and urbanized areas and its application is steadily increasing. Nothing illustrates this better than glyphosate use has increased almost 15-fold between 1996 and 2014 globally (Benbrook 2016). Moreover, according to a study from the United Kingdom 32% of the homeowners apply pesticides in their gardens and glyphosate comprise more than half of them (Tassin de Montaigu and Goulson 2023). Despite the intensive marketing efforts by the industry, an increasing number of studies demonstrated that glyphosate and its residues have unexpected adverse effects on the reproductive success, physiological status and behaviour of non-target organisms such as fishes, toads and arthropods (Bókony et al. 2017; Jarrell et al. 2020; Suppa et al. 2020). Insecticides such as organochlorines are also frequently used as pesticides in urban parks to protect plants from insect pests and these compounds also contribute to the loss of non-target urban arthropods. For example, fipronil, a relatively new insecticide widely used in urban parks, was reported as being responsible for exerting acute toxicity on non-target arthropods and aquatic invertebrates even at very low concentrations (Overmyer et al. 2005; Stevens et al. 2011; Hook et al. 2018; Md Meftaul et al. 2020). Consequently, the shift in plant distribution, increased amount of exotic flora, and application of high amount of pesticides result in altered resources available to herbivores and other organisms that rely on specific plants for food and shelter. Since arthropods are key elements of food webs, their availability is crucial for the quality of urban habitats and determines the presence of species at higher trophic levels (Chatelain et al. 2023). Although different arthropod taxa seem to exhibit heterogeneous responses to urbanization, a global meta-analysis revealed that terrestrial arthropod communities are less diverse and abundant with increased urbanization and that *Coleoptera* and *Lepidoptera* are the most threatened groups (Fenoglio et al. 2020). Another comprehensive study conducted in 180 differently urbanized sites in the city of Innsbruck demonstrated that arthropods' diversity and richness significantly decreased with increasing urbanization both in the tree canopy and in the bush layer (Chatelain et al. 2023).

In summary, the impact of urbanization on wildlife is an extremely complex process. However, the species' responses to urbanization is not universal, may vary across cities (DelBarco-Trillo and Putnam 2023), because the types and strength of anthropogenic stressors, climate, habitat structure, management strategies also differ. Additionally, the individual factors (e.g. light pollution, noise pollution) do not affect the organisms separately but rather cumulatively and interfere with each other, which may deepen the impacts of urbanization even further.

1.2. Breeding performance of urban passerine birds

Many insectivorous bird species nest in urbanized areas and numerous studies have compared their demographic parameters to their conspecifics living more natural habitats (Chamberlain et al. 2009; Seress et al. 2012; Marzluff 2017; Capilla-Lasheras et al. 2022). One common trend observed in urban passerines (order *Passeriformes*) is the earlier onset of breeding compared to their rural counterparts. A study comparing paired urban-rural bird populations (54 species) across Europe found that urban birds started to sing earlier and sang for longer than conspecifics in nearby rural populations (Møller et al. 2015). Consequently, nest-building and egg-laying also often start earlier in urban habitats (Chamberlain et al. 2009). Meta-analyses focusing on reproductive output of birds showed that in general urban birds often have smaller clutch sizes (Chamberlain et al. 2009; Sepp et al. 2017; Capilla-Lasheras et al. 2022), although there are some species that produce more eggs in urban areas compared to natural habitats (e.g. common redstart (*Phoenicurus phoenicurus*; Kuranov 2009). Regarding small insectivorous birds, many of them tend to fledge fewer offspring in urban habitats, for example, house wrens (*Troglodytes aedon*; Grabarczyk et al. 2022), house sparrows (*Passer domesticus*; Seress et al. 2012), great tits (*Parus major*; Seress et al. 2018), blue tits (*Cyanistes caeurelus*; Glądalski et al. 2017) and barn swallows (*Hirundo rustica*; Teglhøj 2017). Additionally, numerous studies have reported that certain individual characteristics of nestlings also differ between urban and natural habitats. For instance, there is a tendency that urban nestlings have different morphological features than their rural counterparts, with a shorter tarsus (Biard et al. 2017), smaller wing lengths (Newhouse et al. 2008) and reduced number of feathers (Sándor et al. 2021). These changes in body parameters can be an adaptive response to urban environment, because the increased temperature may result in increased metabolic costs which may drive shifts to smaller body sizes (Merckx et al. 2018). However, it is generally accepted that body condition at fledging is a good indicator of postfledging survival, i.e. nestlings in higher nutritional condition have higher survival later (Hochachka and Smith 1991; Rodríguez et al. 2016). In urban habitats several studies demonstrated lower body mass at nestling age in a large range of bird species including house sparrows (Seress et al. 2012), house wrens (Newhouse et al. 2008; Baldan and Ouyang 2020; Grabarczyk et al. 2022), great tits (Seress et al. 2018; de Satgé et al. 2019), barn swallows (Teglhøj 2017) and blue tits (Pollock et al. 2017). Corsini et al. (2021) also reported a negative correlation between the degree of urbanization and great tit and blue tit nestlings' growth rate. Moreover, some studies found that urban nestlings have shorter telomeres (Salmón et al. 2016); longer telomeres are associated with longevity, better phenotypic quality and lower mortality rate in many species (Ibáñez-Álamo et al. 2018). Finally, urban nestlings often have paler plumage colour due to the high level of pollution which could also lead to negative impact on their visual signalling later in their lives (Eeva et al. 1998; Leveau 2021).

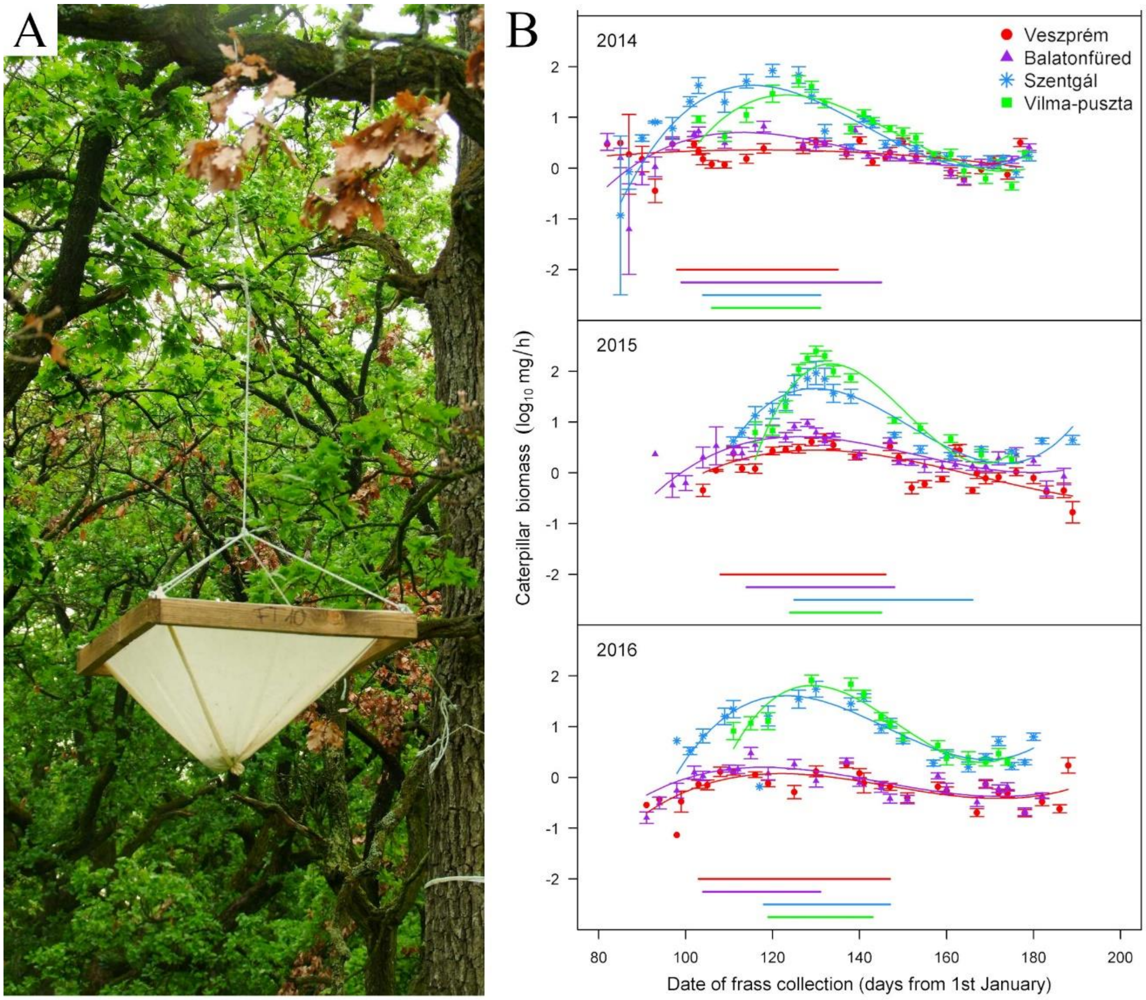
1.3. The food limitation hypothesis

The differences in reproductive success of small passerines between urban and natural environment imply that cities impose a challenge on developing nestlings, with potentially irreversible effects on their lifespan. While there are numerous potential environmental background variables that can explain lower fledgling success and body condition of urban offspring, the food limitation hypothesis seems to be one of the most likely explanations (Chamberlain et al. 2009). This hypothesis proposes that reduced availability of high-quality food for nestlings is the major driver of the reduced reproductive success in urban areas (Seress and Liker 2015; Bailly et al. 2016; Seress et al. 2018, 2020).

Since many passerine birds rely on insects during the chick-rearing period, their presence, abundance and accessibility is crucial for nestling development. Several studies have demonstrated that urban areas generally support fewer (Piano et al. 2020) and smaller (Merckx et al. 2018) insects than natural habitats. However, like in most taxonomic group, insects' responses to urbanization are diverse and taxon-specific (Fenoglio et al. 2020). For many insectivorous birds, it is known that lepidopteran larvae (caterpillars) are the primary nestling food in natural habitats in the temperate climate zone (Perrins 1991; Krištín and Patočka 1997). Caterpillars are widely preferred prey items of songbirds for several reasons. First, caterpillars have soft bodies, which makes them easily digestible for young birds, which is essential given that nestlings have poorer digestive capabilities than adult birds (Caviedes-Vidal and Karasov 2001). Second, caterpillars have especially high nutritional value as they are rich in proteins (Ramsay and Houston 2003) and lipids (Lease and Wolf 2011). Caterpillars also contain large amounts of carotenoids which compounds serve various functions in birds. Carotenoids act as antioxidants, helping to protect cells from damage caused by harmful free radicals (Britton 1995; Costantini and Møller 2008) and also function as immunostimulants supporting immune responses and disease resistance (Blount et al. 2003). Additionally, they are responsible for the red and yellow colours of bird plumage which traits play important roles in mate selection and intraspecific signalling (Delhey et al. 2023). Since carotenoids are synthesized de novo by the plastids of plants as well as some fungi and microorganisms, birds must obtain them through their diet (Goodwin 1984, Latscha 1990). The third reason why caterpillars are preferred for feeding nestlings is that in natural habitats caterpillars are highly abundant in a specific period called ’caterpillar peak’. This time they are found in high amount on plants, trees, and shrubs, providing birds with a consistent and easily accessible food supply. These characteristics of caterpillars make them a high-quality food source for developing nestlings (Kristín and Patočka 1997), hence birds aim to synchronize their breeding time with the seasonal caterpillar peak. The connection between timing of breeding and caterpillar biomass is widely documented in several bird species (Verboven et al. 2001), whereupon mismatching the timing of breeding often leads to lower breeding success (Visser et al. 2004). This is especially well documented in some migratory birds that time their arrival to the local caterpillar peak to maximize breeding success, but in some cases mistiming may lead to population decline. For example, a study found that those pied flycatcher *(Ficedula hypoleuca)* populations that missed the caterpillar peak in their habitat have declined by about 90% (Both et al. 2006). Further evidence for the food limitation hypothesis is that studies which documented poor caterpillar availability in certain habitats such as evergreen forests, agricultural areas, etc., have often also documented inferior breeding success in birds (Bańbura et al. 1994).

So far, in urban habitats, numerous studies have simultaneously investigated caterpillar biomass and breeding success of insectivorous birds and several of them are based on long-term datasets. Frass (insect droppings) biomass is often used as an index to estimate caterpillar biomass (Tinbergen and Dietz 1994; Seress et al. 2018). A frequently-used method to collect caterpillar frass is to hang traps (commonly cheese cloth net attached to a wooden frame; Figure I.1A) into the canopy of individual trees. After drying and sorting the collected droppings, frass mass can be converted into hourly caterpillar biomass of individual trees (mg/h; Seress et al. 2018). Those studies that compared caterpillar biomass between urban and forest habitats found clear evidence for the substantial decrease in peak caterpillar abundance in cities and long-term studies highlighted yearly variation in the degree of this difference (Pollock et al. 2017; Seress et al. 2018; Nadolski et al. 2021). For example, in our urban and forest habitats where my

PhD research was conducted (see detailed description in ***Chapter II***) we found two main features of caterpillar biomass that differ between the two habitat types. First, caterpillar biomass was significantly lower in urban than in forest habitats throughout the studied years (Figure I.1B). The difference between the two habitat types was extremely marked since caterpillar biomass was 8.5 to 24 times higher in forests compared to urban sites (Seress et al. 2018). Second, the forest habitats were characterized by a single large massive caterpillar biomass peak during the nestling rearing period of the first broods and the biomass strongly decreased until the breeding season ended (around July, Figure I.1B). In contrast, in urban habitats we also observed a seasonal decline of caterpillars in some but not all years and/or sites, but this decline was less pronounced because urban trees exhibited several small caterpillar peaks throughout the breeding season (Figre I. 1B; Seress et al. 2018). Based on the above results and in line with the food limitation hypothesis, the reduced availability of caterpillars and their different seasonal dynamics observed in urban environment probably have detrimental effects on nestling development throughout their diet which may contribute to their lower condition and success.



Seress et al. 2018

Figure. I. 1. *(A) Caterpillar frass collector; photo by Csenge Sinkovics, 2014. (B; figure from Seress et. al 2018) Seasonal changes in caterpillar biomass (mg/h) in four years. Red and purple colours represent urban sites, green and blue colours represent forest sites. Dots and whiskers show the mean ± SE of daily caterpillar biomasses. The horizontal lines at the bottom of the panels represent the brood-rearing period (first brood) of great tits for each study site.*

1.4. Nestling diet studies in urban populations

As discussed above, the connection between caterpillar abundance and breeding success has been the focus of intense research. However, nestling diet (i.e. food items that nestlings de facto consume) is less examined. By itself, lower food availability in urban habitats would not necessarily lead to reduced reproductive success, because it is possible that (1) the amount of high quality food may still be enough to allow parents in the cities to provide optimal diet to their offspring, thus (2) reproduction is instead limited by other, stronger effects such as low parental quality, high abundance of parasites, strong predation pressure, and so forth. Therefore, in order to find out whether food availability really can affect breeding success in urban habitats, we need to directly examine the diet of nestlings.

Analysing nestling diet is crucial for gaining a comprehensive knowledge of the nutritional needs of the nestlings as well as gaining insight into the investment and foraging strategies of parent birds (Cholewa and Wesołowski 2011). Earlier studies were often limited to one aspect of the nestling diet (amount or composition), despite the fact that these are both equally important from the point of view of the offspring's development. A sufficient amount of food is obviously necessary for the nestlings as they have high metabolic rates and rapid growth rates, thus, they require a substantial amount of energy and nutrients to develop their body tissues, feathers, and organs. In earlier studies, the quantity of food was commonly measured by the parents' feeding rates (i.e. the per capita feeding visits of the parent birds). However, this is not always a reliable proxy for the amount of food provided to nestlings because there might be a trade-off between prey delivery rate and prey size (e.g. the availability of smaller prey items leads to more visits, Grieco, 2002; Senécal et al., 2021). In addition, sufficient food quality is just as important as food quantity since the lack of essential nutrients may lead to malnourishment, altered feather properties, and also induce oxidative stress in nestlings (Heiss et al. 2009; Eeva et al. 2010; Biard et al. 2017; Bernat-Ponce et al. 2023). Inspecting the types of prey items that nestlings consume also allows researchers to decipher which food sources are preferred in different environmental conditions and how parents optimize their foraging efforts to ensure the survival and growth of their offspring.

There are several traditional diet sampling techniques which all have their benefits and disadvantages and can answer different questions. Formerly, direct observation with binoculars was a frequently used method which is suitable to simultaneously examine parental behaviour and characterise nestling diet on a rough scale (Schwagmeyer and Mock 2008; Seress et al. 2012). Nevertheless, it is hard to avoid the parents getting disturbed by the presence of the observers, and it may be difficult to identify the type and size of the prey items accurately. Tracking diet based on the analysis of stomach contents (e.g. with neck collars; Barba and Gil-Delgado 1990; Pagani-Núñez et al. 2011; Grzędzicka 2018) allows for accurate prey identification, but due to the nature of the sampling technique, it requires quite a lot of practice to avoid the risk of the nestlings getting injured. Extracting and identifying prey's DNA sequences from gut or faecal samples (Orłowski et al. 2015; Jedlicka et al. 2018) is a rapidly developing technique since it provides profound insight into the diet of individual nestlings even at multiple time points and enables the testing of a direct link between fitness traits and consumed prey items. However, this approach may also have estimation bias and there are still some methodological challenges that have to be considered (Deagle et al. 2019). Furthermore, when used alone, DNA sequencing does not provide information on parental activity either. There are some other approaches such as measuring haemoglobin-concentration in the blood of nestlings (Norte et al. 2008; Kaliński et al. 2009, 2019) which indirectly reflect the abundance and quality of food that nestlings receive. However, neither the taxonomic group of the consumed prey items can be identified nor parental activity can be measured with this method alone. Taking photographs or video recordings of the food delivered by the parents is a widespread approach since it allows researchers to easily collect a large amount of accurate data on nestlings' diet (both the composition and amount) as well as parental activity without disturbing them (Seress et al. 2017). Although this method fails to reveal the diet of individual nestlings, instead summarizing the diet for an entire brood, and also does not provide information about the nutrient content of the prey items, it allows researchers to examine parental activity and nestling diet composition and quantity simultaneously, which is beneficial for several reasons. For example, it can reveal the relationship between the time and effort parents invest in foraging and the food they provide to their nestlings. Furthermore, it can shed light on how parents adjust their foraging behaviour in response to changes in food availability or environmental conditions. In summary, there are several methods to choose from to study nestling diet, depending on the specific research question and the available tools and resources.

So far, there are relatively few studies that systematically examined both the composition and amount of nestling diet in relation to urbanization. Furthermore, the previous studies covered mostly one or two breeding seasons, despite the fact that there can be large year-to-year differences in caterpillar abundance between urban and natural habitats (Seress et al. 2018; Nadolski et al. 2021). Moreover, former studies usually were focusing on the first brood of a breeding pair exclusively, even though numerous insectivorous bird species breed multiple times within a season both in urban and in natural habitats. Since caterpillar peaks occur in a relatively short time interval, it is possible that nestlings hatched in second broods may develop under suboptimal food availability conditions, which may also lead to malnourished nestlings. In summary, so far we have incomplete knowledge about how nestling diet and parental activity varies in cities where the annual and seasonal dynamics of caterpillar biomass can be very distinct from natural habitats.

1.5. Thesis objectives

In my doctoral studies, my general aim was to better understand the role of nestling diet in the breeding success of great tits by examining the chick-feeding behaviour of the parents. First, I tested the accuracy and repeatability of the measuring process that I used to quantify nestling food. Second, I compared the composition and amount of nestling food between forest and urban habitat during the first brood of great tits, as these habitats are known to differ significantly in caterpillar availability (as shown in ***Chapter I***, ***section 1.3.***). Third, I also explored how seasonal decline in caterpillar biomass in the two habitat types affects breeding success through nestling diet. The studies below were carried out in collaboration with the Evolutionary Ecology Research Group at the University of Pannonia. I participated in all phases of the work detailed in the following chapters, from planning of the studies to the publishing of the manuscripts.

Objective 1. Insect prey size in nestling diet can be accurately measured from video recordings

Video recordings are commonly used to study the type, amount, and size of food items provided by the parents to their nestlings. Despite its frequent use in science, the accuracy and repeatability of measurements from video recordings usually has not been examined and validated. Having a repeatable measurement is crucial for ensuring accuracy, reliability and reproducibility in data collecting, thus, in ***Chapter III*** we assessed some aspects of the reliability of measuring birds' prey size from screenshots of video recordings. To test the accuracy of the method, we created artificial plasticine caterpillars and compared their real size and volume to estimates measured from screenshots taken in a way that is identical to the video recordings we used during our field studies (***Chapters IV and V***). Furthermore, we also tested within-observer reliability, where one person measured real prey items from video recordings twice, as well as among-observer reliability, where three people measured each prey item once and compared the measurements.

Objective 2. Effects of urbanization on nestling diet in great tits: the importance of food composition and large caterpillars

In ***Chapter IV*** we investigated the relationship between habitat urbanization, nestling diet and breeding success. The starting point of this study was that Seress et al. (2018) found that in our study system the biomass of caterpillars living in tree canopies and the breeding success of great tits markedly differed in urban habitats compared to forests in four consecutive years. During the chick-rearing period of first broods, caterpillar biomass was up to 24 times lower in urban than in forest study sites. In parallel, urban pairs had significantly smaller clutches, fledged significantly fewer and smaller offspring per breeding attempt and experienced more frequent starvation-related brood reduction. However, that study did not investigate whether and how low environmental caterpillar availability affected nestling diet. According to the food limitation hypothesis the shortage of high-quality nestling food (caterpillars) is a major factor responsible for the reduced reproductive performance in urban insectivorous birds (see above). To study this hypothesis, we compared the diet of great tit nestlings in the same urban and forest habitats in three consecutive years. For this purpose, we collected video observations on parents' food provisioning behaviour and determined the type and amount of nestling food they delivered using our validated method described in ***Chapter III***.

Objective 3. Comparison of nestling food between first and second broods of great tits in urban and forest habitats

The background of the third study is that in the aforementioned study (Seress et al. 2018) we observed that the biomass of caterpillars declines during the birds' breeding season both in urban and in forest habitats. Following the food limitation theory presented above (***Chapter I, section 1.3***), we predicted changes in the composition and/or amount of the nestling diet, and also a decrease in reproductive success as the breeding season progresses within both habitat types. To investigate this, we selected urban and forest great tit pairs that had two broods within the same breeding season and compared nestling food composition, amount and breeding success between their brood types (first versus second brood).

CHAPTER II

General field methods

2.1. Study species

The great tit is a small (13.7-22.0 g, Vincze 2018) bird in the avian order *Passeriformes* and the family *Paridae*. It has a wide distribution across much of Eurasia and can be found across all of Europe. It is generally resident in Hungary and does not migrate except in extremely harsh winters (Magyar Madártani és Természetvédelmi Egyesület, *online*). The great tit occupies a wide range of habitats, from natural habitats such as open deciduous woodland, mixed forests, and forest edges to various human-transformed areas like farmlands, urban public parks, and gardens (Magyar Madártani és Természetvédelmi Egyesület, *online*). It is predominantly insectivorous in the summer, but in the winter it also consumes a broad range of seeds, and even attacks and partially eats small hibernating bats (Estók et al. 2010).

In natural habitats, the great tit nests in cavities, burrows, crevices or decays and may breed twice a year. In urban settlements it may occupy almost any closed space or hollow (e.g. post boxes, fence pipes) and it readily nests in artificial nest boxes. In general, the base of the great tit nest is constructed of green moss, but the nest cup is lined with fine material such as animal hair (Figure II.1A; Deeming and Reynolds 2015). Those pairs that breed in human settlements often use artificial wool-like materials for nest lining (e.g. yarn, pillow filling, strings; James Reynolds et al., 2019). Although the great tit is socially monogamous, extra-pair copulations occur particularly often in urban habitats (Pipoly et al. 2019). The eggs are brownish spotted on a white base, but variation in egg pattern can be significant even within the same clutch (Figure II.1A; Gosler et al. 2005). In Hungary, clutch size varies between 5 and 14 eggs depending on habitat and season (Haraszthy 2019). Females lay one egg per day and incubate them for approx. 14 days. Males do not participate in the incubation of eggs. After hatching, both parents take cares of the nestlings who stay in the nest for 20 to 22 days (Haraszthy 2019). After fledging, parents (mainly the male) lead and feed the youngs until they become independent (Haraszthy 2019).

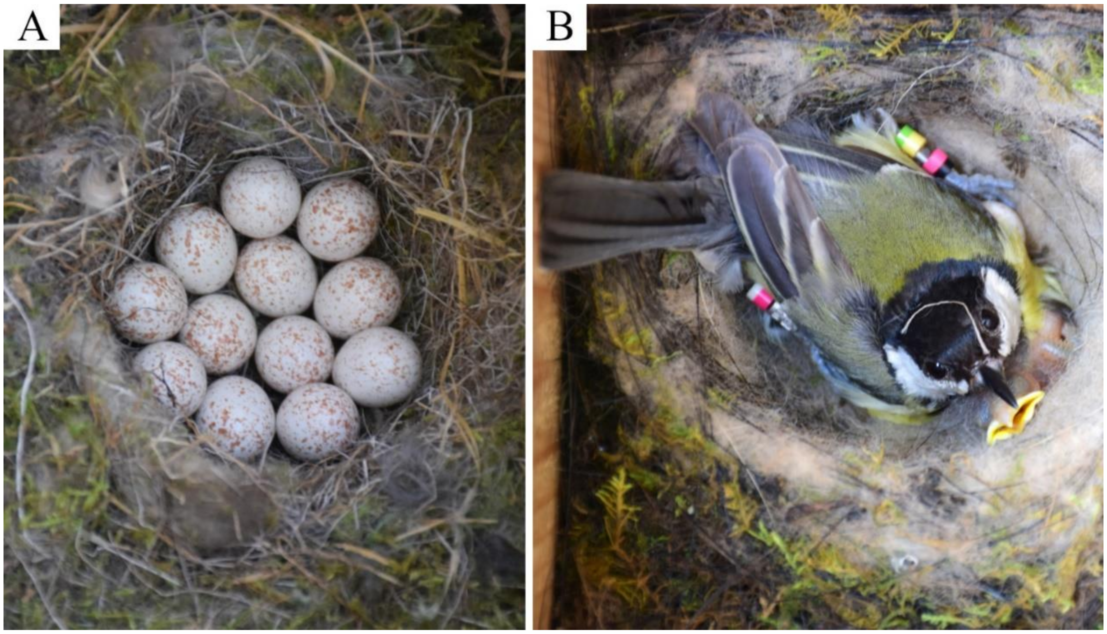
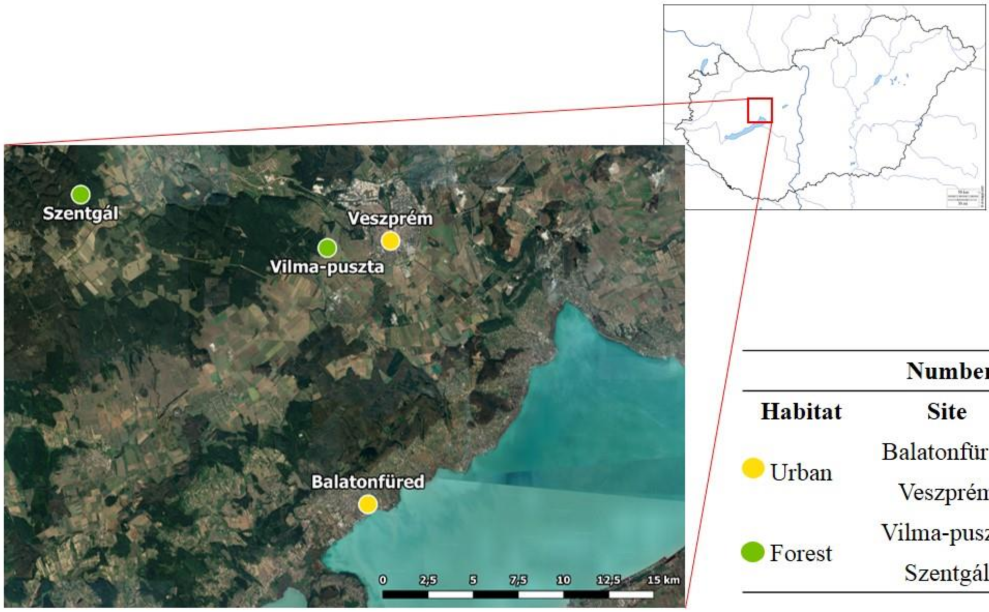


Figure II.1. *(A) Great tit nest with spotted eggs. (B) Colour-ringed female great tit is sitting on eggs and few days old nestlings (photos by Csenge Sinkovics).*

2.2. Study sites

We have been studying the ecology of great tits breeding in artificial nest boxes at two urban and two forest sites in Hungary since 2013 (Figure II.2). The urban study sites are located in Veszprém (47°05’17”N, 17°54’29”E) and Balatonfüred (46°57’30”N, 17°53’34”E), where the nest boxes are placed in public parks, a cemetery, and university campuses where vegetation consists of both native and exotic species. One of the forest study sites is located at Vilma-puszta (c. 3 km from the edge of Veszprém; 47°05'06.7"N, 17°51'51.4"E) dominated by downy oak (*Quercus pubescens*) and South European flowering ash (*Fraxinus ornus*). The other forest study site (47°06'39.75"N, 17°41'17.94"E) is located 3 km away from the nearest human habitation, Szentgál, and c. 20 km away from Veszprém. This study site is dominated by beech (*Fagus sylvatica*) and hornbeam (*Carpinus betulus*). In each study site we installed on-site weather stations to collect hourly data of the ambient air temperature.



		Number of nestboxes		
Habitat	**Site**	**2014**	**2015**	**2016**
● Urban	Balatonfüred	77	76	74
	Veszprém	79	77	77
● Forest	Vilma-puszta	88	87	87
	Szentgál	94	94	88

Figure II.2. *The map of Hungary, where the spots are indicating the urban (yellow) and forest (green) study sites. The table shows the number of nest boxes belonging to each habitat and study site in the studied years. The map was created with QGIS v. 3.20.1.(QGIS Development Team 2021), the satellite image was retrieved from Google Maps (Google 2021) and the hydrographic map was downloaded from d-maps.com (Anon 2021).*

2.3. General field protocol

Between 2014 and 2016 we followed the breeding performance of the above two urban and forest great tit populations from March to July. We checked the nest boxes at least every 3 to 4 days throughout each breeding season to determine laying dates, clutch sizes, hatching dates, and brood sizes of breeding great tits. We determined nestling age (hatch day = 1 day old) based on the size, appearance and feather growth status of them using a photographic guide. When the oldest nestling in a brood reached the age of 8 to 12 days we made one video recording at the nest to examine the nestling-feeding behaviour of parent birds. We selected this age period because earlier studies showed that the food demand of the nestlings is the highest around this age (Betts 1955; Van Balen 1973; Corsini et al. 2021). For the following studies we made one 60 minutes long recording covering the whole day period (between 8 and 18:15, see means ± SE in each study) because this length is suitable for characterizing the variation in parental provisioning in great tits (Pagani-Núñez and Senar 2013) and differences between pairs are also detectable (Murphy et al. 2015). At the start of each video observation we mounted a small camera (GoPro HD HERO 2 or 3) into a black plastic box outside of the nest box, 15 cm from the entrance hole (Figure II.3). These plastic boxes serve as camouflage for the cameras, and are constant accessories of our nest boxes; breeding birds are familiar with them. Our earlier study showed that the presence of the cameras in the plastic boxes does not have detectable effects on the parents' behaviour (Seress et al. 2017). A wooden shelf below the entrance hole is also attached to the nest boxes, where parent birds often pause for a moment before entering the nest box. Since ambient temperature may influence food searching behaviour of the parent birds (Geiser et al. 2008) we recorded the actual temperature during each video recording to control for its effect later in the analyses.

Figure II.3. *Nest box design. We placed a wooden shelf in front of the entrance hole which allows the birds to pause for a moment. We attached a black plastic box for camouflaging the camera. Photo by Csenge Sinkovics, 2019.*

To avoid disturbing the parents' behaviour the observers who mounted the cameras stayed away from the nest during the recording periods. The number of nestlings was counted before the start of each video recording. In the days after the video recording was made at a nest we captured parent birds using a manual nest box trap (Seress et al. 2017). We ringed the parents with a unique combination of a numbered metal ring and three plastic colour rings and determined their sex and age based on their plumage coloration (Svensson 1992). We also measured their left tarsus length with a Vernier caliper (± 0.1 mm), their wing length with a wing ruler (± 1 mm) and their body mass with a Pesola spring balance (± 0.1 g). Those adult birds that were ringed in previous broods (either from the same year or from previous years) and were successfully identified from the actual video recording were not captured again. Nestlings were also ringed with a numbered metal ring and measured with the same process circa a week prior to fledging (i.e. 14-17 days after hatching). After ringing the nestlings, we did not check the nest boxes to avoid the risk of premature fledging. Shortly after the expected day of fledging (approx. 22 days after the first nestlings hatched) we emptied the nest boxes and recorded the number of nestlings that died between the ringing and fledging period.

CHAPTER III

INSECT PREY SIZE IN NESTLING DIET CAN BE ACCURATELY MEASURED FROM VIDEO RECORDINGS

Csenge Sinkovics, Gábor Seress, Virág Fábián, Krisztina Sándor & András Liker

ABSTRACT

Video recordings are commonly used to study the types, amount, and size of food items provided to nestling birds. However, the accuracy and repeatability of estimates of the size of food items from video recordings has not been examined. We assessed three aspects of the reliability of measuring prey size from video recordings of Great Tits *(Parus major)* provisioning nestlings. To test the accuracy of measurements of prey size (length and width) used to determine prey volume, we moulded artificial plasticine caterpillars and compared their size and volume as determined using measurements of length and width on screenshots of video recordings (using the vertical diameter of nest box entrance holes as a size reference) to their actual size and volume. We also examined within- and among-observer repeatability of measurements of the size and volume of actual prey items delivered to nestlings by adult Great Tits. We found that observers were able to accurately measure prey size and determine volume, with high agreement between the actual size and volume of plasticine caterpillars and the size and volume as determined from measurements made on screenshots from video recordings ($r_{ICC} = 0.99$). In addition, within- and among-observer repeatability were also high ($r_{ICC} = 0.98$ and 0.93, respectively). Overall, our results suggest that the size of prey items delivered to nestlings by adults in video recordings can be accurately measured and those measurements, in turn, can be used to accurately determine the volume of those insect prey.

This chapter is an extended and modified version of the research article „Csenge Sinkovics, Gábor Seress, Virág Fábián, Krisztina Sándor & András Liker (2018): Obtaining accurate measurements of the size and volume of insects fed to nestlings from video recordings. *Journal of Field Ornithology* 89(2): 165-172”.

3.1. Introduction

As described in ***Chapter I*** the number and condition of nestlings is an important component of reproductive success for birds, and – among other factors – critically depend on the quality and amount of food provided by the parents (Naef-Daenzer and Keller 1999). Food quality is usually studied by identifying components of nestling diet, whereas the quantity of food is most commonly described by feeding rates. However, feeding rate is not always a reliable proxy for the amount of food provided to nestlings because there might be a trade-off between prey delivery rate and prey size (e.g. the availability of smaller prey items leads to more visits, Grieco, 2002; Senécal et al., 2021). As introduced in ***Chapter I***, several methods have been used in the past to investigate composition and quantity of nestling food, including direct behavioural observations (Schwagmeyer and Mock 2008, Seress et al. 2012), neck-collars (Barba and Gil-Delgado 1990, Pagani-Núñez et al. 2011), artificial nestling gape (which is a tweezer-like device mimicking a nestling's bill so the parents put preys in this artificial nestling; Betts 1951; Gibb and Betts 1963), and faecal analysis (Deagle et al. 2010; Orłowski et al. 2015; Moran et al. 2019). With rapid technological advancements, applying small video cameras (near or inside the nests) is also becoming increasingly popular, as this approach allows researchers to collect a large amount and accurate data on birds' diet without disturbing them (Colombelli-Négrel and Kleindorfer 2010; Seress et al. 2017). A particularly attractive advantage of taking video recordings is that these allow researchers to estimate the size of individual food items. In general, however, size estimation requires something to which the size of food items can be compared. For this purpose, some studies used e.g. the birds' beak size as a reference (e.g. Navalpotro et al. 2016), whereas others placed a scale bar above the entrance holes of nest boxes (García-Navas and Sanz 2010). Investigators have also determined prey size in different ways, e.g., some have only used broad size categories (Seress et al. 2012), others estimated prey length (Banbura et al. 2001, García-Navas and Sanz 2010), and still others have estimated the length and width of food items and calculated prey volume (Blondel et al. 1991; Slagsvold and Wiebe 2007; Wiebe and Slagsvold 2014).

Although analysis of video recordings can provide useful information about both the composition and size of food items provided to nestlings, the repeatability and reliability of this method has not been tested. However, having a repeatable measurement is crucial for ensuring accuracy, reliability, reproducibility, and the ability to compare and analyse data. Particularly, if more than one person are involved or the measurement is made with different methods. Thus, our objectives were to 1) determine how often observers can identify prey items and determine their size from video recordings of Great Tits (*Parus major*) provisioning their young, 2) test the accuracy of prey size measurements by comparing the actual sizes of known-sized artificial food items to their sizes as measured from screenshots of video recordings, and 3) test the repeatability of the size measurements both within and among observers.

3.2. Methods

3.2.1. Determining the type and volume of prey items from video recordings

For this study we followed the general field protocol (detailed description in ***Chapter II***) and collected a 60 minutes long video sample per breeding pair in nestling age of 8-12 days (mean ± SE = 9.6 ± 0.1) in 2014. In a nutshell, we concealed a small camera near the nest boxes' entrance hole (Figure II.3) and went far away during the observation period to avoid potential disturbance. We visually scanned 53 video recordings using VLC media player 2.1.5. (Free Software Foundation) and took a screenshot of each feeding event when a parent bird held a prey item in front of the entrance hole (mean = 21.9 ± 1.7 feeding events per video recording; Figure III.1). Adult Great Tits are usually single prey loaders (Kluijver 1950), and in this study we did not record any feeding event when a parent carried multiple prey items. From screenshots, we determined prey type and also measured the size of food items that were clearly visible. We divided food items into three categories: (1) caterpillar, (2) other arthropods, and (3) non-arthropods (e.g., seeds and eggshells). We then used the software Fiji (Schindelin et al. 2012), and with its 'Segmented Line' function we measured the length and width of each prey item to the nearest 0.001 mm (excluding wings and legs), and used the vertical diameter of the entrance hole (32 mm and clearly visible in each screenshot) as a size reference (after drawing the vertical line across the entrance hole using the 'Analyze menu' → 'Set Scale' function). We measured the length of food items, and their average width was calculated as the mean of three measurements at each third of the item's length because width can vary along the body of some types of prey (Figure III.1). We then calculated prey volume, assuming prey had the shape of a cylinder (Slagsvold and Wiebe 2007), using the following equation:

$$V = \pi l(0.5w)^2$$

where V is prey volume, and l and w are the length and average width of a prey item, respectively.

Figure III.1. *The process of measuring prey size. The length of prey items was measured once along the middle axis (white dotted yellow line on the caterpillar), and prey width was measured three times along each third of the prey's length (black lines). The blue arrow shows the height of the entrance hole (size reference).*

3.2.2. Measuring the volume of artificial caterpillars

To test the accuracy of measuring prey size from images, we moulded 40 artificial caterpillars from coloured plasticine to resemble living *Lepidoptera* larvae (Figure III.2.A), which are the main component of the diet of nestling Great Tits in our study population and other populations (Perrins 1991, Sinkovics 2014). Because our earlier field observations revealed that adult Great Tits delivered caterpillars between 2.67–36.17 mm in length and between 1.19–8.35 mm in width to nestlings, the size of plasticine caterpillars varied within these ranges (Sinkovics 2014). Plasticine caterpillars were made in the characteristic curved position similarly to that when birds hold caterpillars in their beaks. We held the artificial caterpillars with tweezers (to mimic a bird's beak; Figure III.2.B) at the front of a nest box entrance and recorded these presentations with a video-camera placed in the camera-box used to record provisioning behaviour (see above). Artificial caterpillars were presented in random order. The measuring process was the same as described above (i.e., we took screenshots and measured length and average width to calculate volume), and the person doing the measuring did not know the actual size of these artificial food items. Finally, we measured the length and width of the plasticine caterpillars with caliper and calculated their true volume.

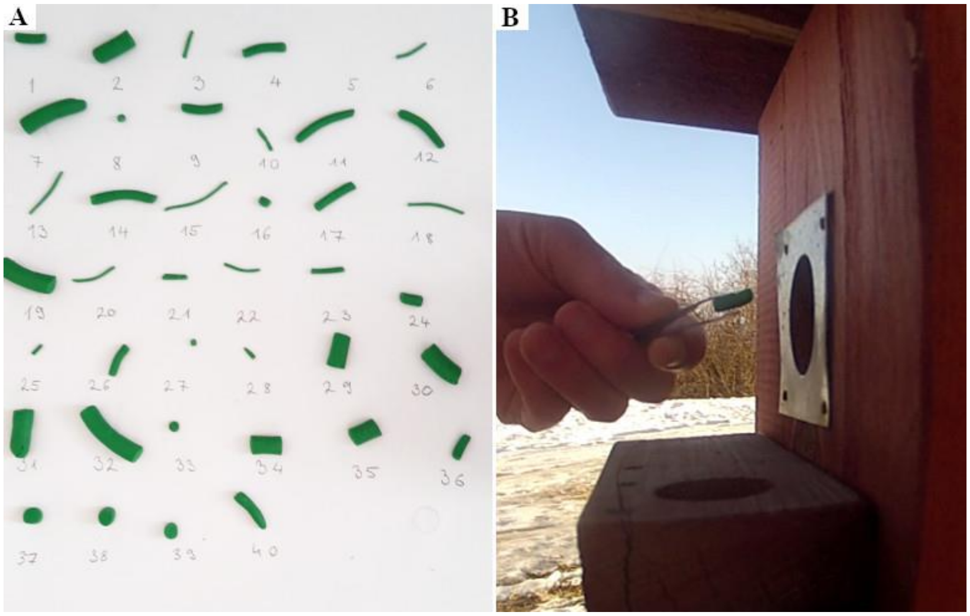


Figure III.2. *(A) Different length and width caterpillars made from green plasticine that are (B) shown to the camera (GoPro Hero 2) with a tweezer mimicking great tits' beak. Photos by Csenge Sinkovics.*

3.2.3. Within- and between-person reliability of prey size measurements

To test whether the measurements of actual prey items from video recordings (described above) were reproducible, we selected 40 prey items from 12 video recordings that were clearly visible. These prey items were selected to represent the whole prey-size spectrum. For testing within-observer reliability, one person measured these items twice, whereas, for testing among-observer reliability, three people measured each item once.

3.2.4. Statistical analyses

We used intraclass correlation (ICC) to test the repeatability between measurements (Lessells and Boag 1987, Koo and Li 2016). Various ICC coefficient (r_{ICC}) values were proposed as thresholds for reliable measurements: for example, Lee et al. (1989) suggest that ICC indicates a reliable method if the lower limit of the 95% confidence interval of r_{ICC} is at least 0.75; Chinn (1991) recommends that a useful measurement should have an r_{ICC} of at least 0.6; Koo and Li (2016) suggested that an r_{ICC} between 0.5 - 0.75 indicates moderate, 0.75 - 0.9 indicates good, and > 0.90 indicates excellent reliability. Here we used the most often-used criterion, i.e., whether r_{ICC} was significantly higher than 0.75.

In addition to calculating ICCs, we also tested whether there was any consistent bias between repeated measurements by comparing the mean values of these measurement series (Lee et al. 1989). In the artificial caterpillar experiment and within-observer reliability test where two sets of measurements were compared, we used paired *t*-tests to examine possible differences between the means. In the among-observer reliability test with three observers, we used linear mixed-effects models (LMM, using package ‘nlme’), where the dependent variable was prey volume, the explanatory variable was observer ID (i.e., the IDs of the three people who measured the same prey items), and the random factor was the prey item ID. To summarize, in each case, we used ICC to examine the correlation between two series of measurements as well as using a paired *t*-test or LMM to compare the means of the measurements. Statistical analyses were conducted using R statistical software (version 3.2.2). ICC estimates and their 95% confident intervals were calculated using the 'irr' R package.

3.3. Results

We identified 68.3% of the prey items from the videos of Great Tits provisioning nestlings, and were able to measure the volume of 32.4% of the prey items ($N = 1169$ feeding events). When prey type, prey size, or both could not be determined, adults either entered nest boxes too fast, resulting in a blurry image, or held prey items so they were not clearly visible (e.g., partially blocked from view by a bird’s bill).

Comparison of the true volume of plasticine caterpillars with their volume as determined using measurements on screenshots of video recordings revealed that our method allowed accurate estimates of prey volume. The r_{ICC} values were high (Table III.1, Figure III.3A) and we found no significant difference between the means of the two sets of measurements (Table III.2). We also found that estimates of prey volume were highly repeatable. The r_{ICC} values were high for both within- and among-observer repeatability (Table III.1., Figure III.3B-E), and we found no significant differences between mean volumes estimated by repeated measurements made by either the same or different observers (Table III.2). Estimates for the volume of smaller prey items are more accurate than for bigger ones (Figure III.3.B-E).

Table III.1. *Intraclass correlation (ICC) tests of the repeatability between actual volumes and those determined using measurements from screenshots from video recordings, and of within- and among-observer measures of prey volume from video recordings. For plasticine caterpillars (N = 40), one person first measured length and width from a screenshot and then measured their real size with a caliper. For within-observer reliability, one person measured each prey item (N = 40) on screenshots twice and, for among-observer reliability, three people measured the same prey item once. We tested the null hypothesis that $r_{ICC} > 0.75$, so the reported P values refer to the significance of this test.*

	Intraclass correlation			
Comparison	r_{ICC}	95% confidence interval of r_{ICC}	*F*	*P*
Plasticine caterpillars	0.99	0.985-0.995	31.6	< 0.001
Within-observer reliability	0.98	0.97-0.99	16.2	< 0.001
Among-observer reliability	0.93	0.90-0.96	4.3	< 0.001

Table III.2. *Comparison of actual volumes of plasticine caterpillars and those determined using measurements from screenshots of video recordings, and the within- and among-observer reliability of determining prey volumes determined using measurements from screenshots. We used paired t-tests to compare plasticine caterpillars and within-observer repeatability, and a linear mixed-effect model for among-observer repeatability.*

Comparison		Mean difference or intercept (mm^3)	SE	*t*	*P*
Plasticine caterpillars	-	0.92	7.42	0.1	0.90
Within-observer reliability	-	-1.86	6.26	-0.3	0.77
Among-observer reliability	Intercept (Observer 1)	225.08	34.68	6.5	< 0.001
	Observer 2	1.85	12.78	0.1	0.89
	Observer 3	-4.33	12.78	-0.3	0.74

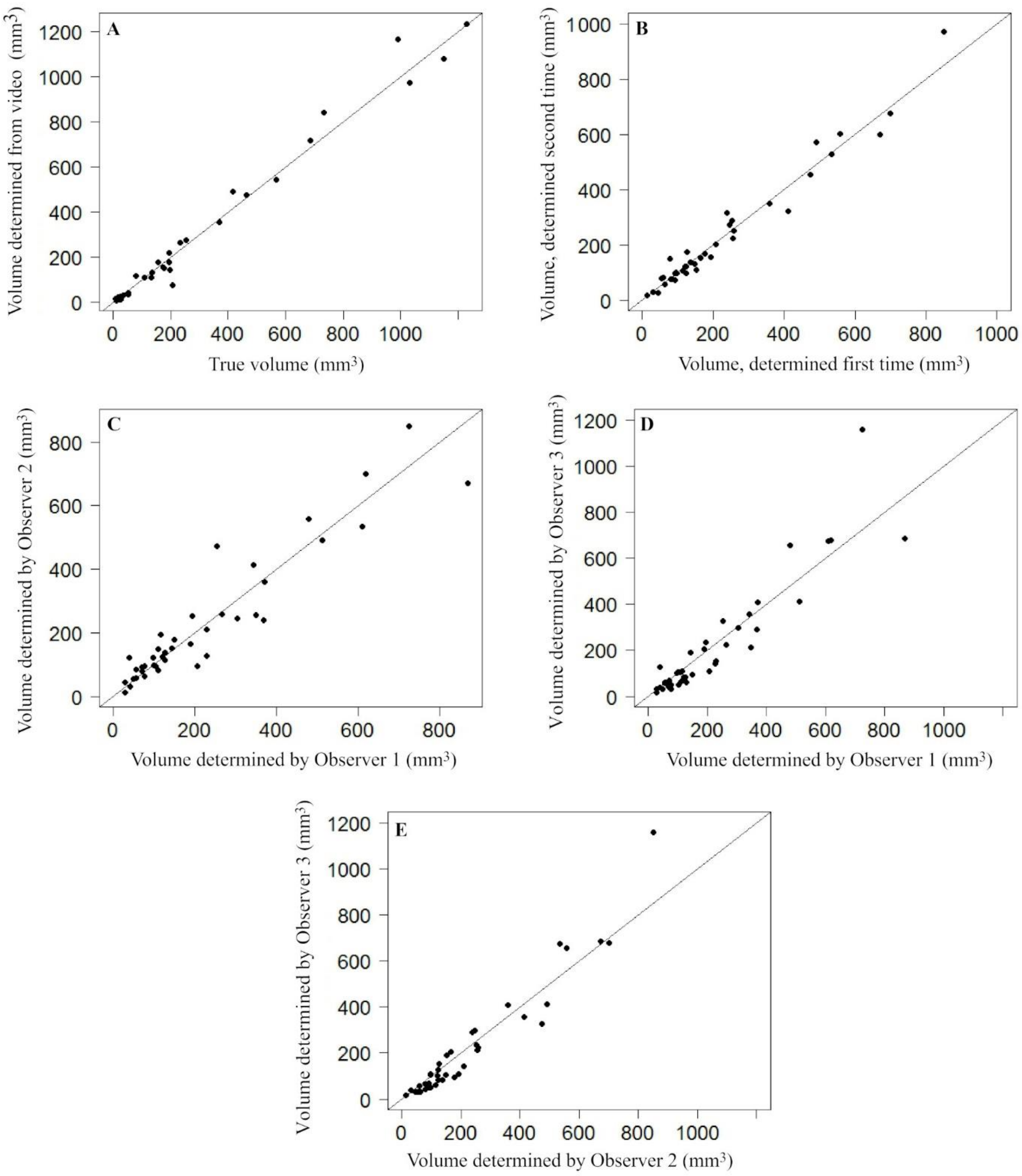


Figure III.3. *Consistency of volume estimates for (A) plasticine model caterpillars and (B–E) natural prey items of Great Tits. (A) Relationship between the size of plasticine caterpillars measured from images and their real size measured with calipers. (B) Within-observer reliability when one observer measured each object twice. (C–E) Among-observer reliability when three observers measured each object. The black lines show the hypothetical perfect match, that is, when measurements made by observers were identical.*

3.4. Discussion

Our plasticine-caterpillar experiment confirmed that the volume of prey items provided to nestlings can be accurately determined using measurements made on screenshots from video recordings, and our reliability analyses revealed that measurements were highly repeatable and unbiased both within and among observers. We also found that the diameter of nest box entrances can provide a good size standard for measuring prey size. Although we tested this method with great tits nesting in nest boxes, we believe that our method can also be used with open-cup-nesting species if a known-sized, unobtrusive, and camouflaged object that can be used as a size reference is placed near nests.

A disadvantage of using a camera outside of nest boxes in our study was the difficulty in determining the type and size of prey items because adults either entered nest boxes too fast or preys were not clearly visible. We suggest three possible ways to overcome these issues. First, video recordings in some studies have been made using infrared cameras placed inside nest boxes (O'Connor et al. 2010, 2014; Pagani-Núñez and Senar 2014; Navalpotro et al. 2016). This may make identification and measurement of prey items more effective because video recorders can be placed in a more favourable position (e.g., in front of adults rather than on the side) and because adults may move more slowly once they enter a nest box. Second, Currie et al. (1996) also used video-cameras placed outside of nest boxes, but attached a small wire cage to the front of the entrance. Because parent birds could only access their nest through the wire cage, they moved more slowly and improved the likelihood that prey items could be identified and their size measured. Using this method, Currie et al. (1996) were able to identify 94.4% of the prey items delivered to nestling Great Tits from video recordings.

Finally, the number of prey items that can be measured can be increased by extrapolating volume from estimates of size. For example, we recorded several feeding events where a prey item was clearly visible, but its size could not be measured because the parent bird did not hold it right in front of the entrance hole that we used to scale prey size. In many such cases, however, we were able to estimate approximate prey size relative to the length (from the skull to the bill tip) and height (at the anterior edge of the nostril) of bird bills and then used these values to estimate prey volume (Sinkovics et al., unpublished data). To do this, we created four length categories, including small (evidently shorter than the bill, by at least one-third of bill length), medium (approximately the same length as the bill), large (longer than the bill by at least one-third of bill length), and extra-large (at least twice as long as the bill), and three width categories, including thin (evidently thinner than bill height, by at least one-third of bill height), medium (approximately the same width as the bill), and thick (wider than bill height by at least one-third of bill height), and then placed the unmeasured prey items into one of 12 size categories (small × thin, small × medium, and so on). Then, we placed the measured prey items into the same categories using their exact length (small ≤ 8 mm, medium = 8–16 mm, long = 16–24 mm, and extra ≥ 24 mm) and width (thin ≤ 3 mm, medium = 3–6 mm, and thick ≥ 6 mm) and calculated the average of the measured volumes for each category. Finally, we assigned these average volume values to the unmeasured prey items (that were categorized only by comparison to bill length and height). Using this method, we were able to estimate the volume of a greater percentage of prey items (57.4% rather than 32.4%). We used the average length and height of the bills of Great Tits in European populations (12 and 4.5 mm, respectively; Zając 1999, BWPi 2006) to create the size categories, but investigators should measure the bills of birds in their own study populations because bill sizes may differ among countries (Bosse et al. 2017), populations (Ulfstrand et al. 1981), and habitats (Giraudeau et al. 2014). It is important to note here, that we further developed this extrapolation method in our later researches (detailed in ***Chapter IV***).

In conclusion, we found that accurate measures of the volume of prey items can be made from video-screenshots, allowing investigators to characterize the provisioning efforts of adults by prey volume rather than just provisioning rates, at least for single prey-loading species that deliver one food item per feeding visit. We also found that accurate measurements can be made by multiple observers, given our high among-observer repeatability, when observers are provided with a detailed description of the protocol for making measurement. Nevertheless, we strongly recommend that researchers always check for among-observer bias when more than one observer collects the data because the accuracy of measurements might differ between or among observers. Finally, our results show that the location of video-cameras (i.e., outside vs. inside nest boxes) is important and can potentially limit the ability of observers to identify and accurately measure the size of prey items delivered to nestlings by adults.

CHAPTER IV

EFFECTS OF URBANIZATION ON NESTLING DIET OF GREAT TITS: THE IMPORTANCE OF FOOD COMPOSITION AND LARGE CATERPILLARS

Csenge Sinkovics, Gábor Seress, Ivett Pipoly, Ernő Vincze & András Liker

ABSTRACT

Rapidly increasing urbanisation is one of the most significant anthropogenic environmental changes which can affect demographic traits of animal populations, for example resulting in reduced reproductive success. The food limitation hypothesis suggests that the shortage of high-quality nestling food in cities is a major factor responsible for the reduced reproductive performance in insectivorous birds. To study this explanation, we collected data on the parental provisioning behaviour of urban and forest great tits *(Parus major)* in three years that varied both in caterpillar availability (the main food of great tit nestlings) and in reproductive success of the birds. In all years, urban parents provisioned caterpillars in a smaller proportion to their nestlings, but the total amount of food per nestling (estimated by the volumes of all prey items) did not differ between habitats. In the two years with much lower reproductive success in urban than forest habitats, urban parents had higher provisioning rates, but provided more non-arthropod food and brought smaller prey items than forest parents. In the year with reduced habitat difference in reproductive success, urban parents were able to compensate for the scarcity of caterpillars by provisioning other arthropods rather than non-arthropod food, and by delivering larger preys than in the other years. Specifically, in this latter year, caterpillars provisioned by urban pairs were cc. twice as large than in the other two years, and were similar in size to caterpillars provisioned in the forest broods. These results show that although urban great tit parents can provide the same quantity of food per nestling as forest parents by reducing their brood size and increasing the per capita feeding rates for nestlings, they cannot compensate fully for the scarcity of high-quality preys (caterpillars) in poor years. In some years, however, favourable conditions for urban caterpillar development can greatly reduce food limitation in cities, allowing urban birds to achieve higher reproductive success. We suggest that urban green areas designed and managed in a way to facilitate conditions for phytophagous arthropods could improve habitat quality for urban birds.

This chapter is an extended version of the research article „Csenge Sinkovics, Gábor Seress, Ivett Pipoly, Ernő Vincze & András Liker (2021): Great tits feed their nestlings with more but smaller prey items and fewer caterpillars in cities than in forests. *Scientific Reports* 11: 24161”.

4.1. Introduction

As expounded in ***Chapter I,*** the availability of caterpillars may play a key role in the reproductive success of passerine birds. However, the abundance of caterpillars – similarly to many other insects – has been dramatically declining in many urban areas compared to more natural habitats (Seress et al. 2018; Fenoglio et al. 2020; Piano et al. 2020; Nadolski et al. 2021). Urban breeding birds can adapt to this reduced natural food supply in at least four non-mutually exclusive ways. First, the negative effects of food limitation on nestling development and survival can be mitigated by laying smaller clutches. This strategy can reduce the detrimental effects of food limitation as fewer nestlings require less amount of food. According to this expectation, studies commonly find smaller clutches in urban than in non-urban insectivorous bird populations (Chamberlain et al. 2009; Sepp et al. 2017; Capilla-Lasheras et al. 2022).

Second, urban parents may increase their chick-feeding activity to provide a sufficient amount of natural food for their nestlings if large prey items are scarce, for example, due to the smaller size of urban arthropods (Miyashita et al. 1998; Ishitani et al. 2003; Merckx et al. 2018). Supporting this scenario, smaller food items were reported in urban than non-urban environments in the nestling diet of blue tits (Pollock et al. 2017; Jarrett et al. 2020) and house sparrows (Seress et al. 2012), and an increased chick-feeding frequency was measured in urban relative to more natural habitats, for example, in great tits (Isaksson and Andersson 2007; Sinkovics 2014) and blue tits (Pollock et al. 2017). Furthermore, to keep up the rate of nestling food deliveries urban parents may also have to fly further from their nest (Jarrett et al. 2020), similarly to what was found in blue tits breeding in good versus poor habitats in more natural environments (Tremblay et al. 2005). Note, however, that a higher provisioning rate of small prey may not necessarily compensate for the reduced amount of large arthropod prey items in nestlings' diet. A study in urban house sparrows showed that the frequency of large arthropod prey items in the diet, and not parents' feeding rates *per se*, predicted brood size and nestling body mass (Schwagmeyer and Mock 2008), which can be related to the size-dependent variation in arthropods' calorific or nutritional content. For example, Lease and Wolf (Lease and Wolf 2011) found that the lipid content of arthropods shows an isometric scaling relationship with respect to their body mass, resulting in a proportionately larger quantity of nutrients (e.g. lipids) in large compared to smaller arthropods.

Third, urban parents might try to compensate for the relative scarcity of high-quality diet components, like caterpillars and other arthropods, by provisioning anthropogenic food items (e.g., garbage, bird food) to their offspring. Such altered nestling diet has been reported in several urbanized bird species, including blue tits (Pollock et al. 2017; Jarrett et al. 2020), great tits (Riddington and Gosler 1995), common starlings (*Sturnus vulgaris;* Mennechez and Clergeau 2006) and Florida scrub-jays (*Aphelocoma coerulescens;* Shawkey et al. 2004). Although anthropogenic food sources are typically abundant and easily accessible in urban environments (Robb et al. 2008), their nutritional composition is likely to be inadequate to support optimal nestling development (Mennechez and Clergeau 2006; Sauter et al. 2006). Indeed, the most common food items at bird tables (e.g. birdseed, tallow, peanut cakes, or bread crumbs) are rich in fat and carbohydrates, making them a good source of energy for adults in winter, but typically contain low amounts of nutrients like protein or calcium (Graveland and van Gijzen 1994; Heiss et al. 2009) which are fundamental growth-limiting factors for nestlings in spring (Ricklefs 1983). Thus, the altered palette of nestling food may result in nutrient deficiency rather than caloric restriction for urban nestlings. In line with this assumption, a number of studies reported links between reduced breeding success and increased amount of plant material (Peach et al. 2008), fat (Johnston 1993), or human refuse (Mennechez and Clergeau 2006) in nestlings' diet in birds that normally rely on arthropod-based food.

Based on the above findings, the availability of different, natural food types is a key factor for insectivorous birds that determines the success of nestling rearing. As introduced in ***Chapter I***, we have explored caterpillar biomass and breeding success of great tits in our urban and forest study sites across years and found both annual and habitat differences. We found strongly decreased caterpillar biomass in the canopies of urban relative to forest trees (the yearly mean ± SE of hourly caterpillar biomass (mg/h)) during the nestling rearing period was ranging from 1.67 ± 0.1 to 5.86 ± 0.54 in the urban sites, and from 50.09 ± 6.25 to 122.96 ± 13.93 in the forest sites, see Figure 3. in the cited publication (Seress et al. 2018). In parallel, great tits laid smaller clutches and produced fewer and smaller fledglings (as measured at the age of ringing, 15 ± 1 days after hatching) in urban study sites, although the extent of habitat difference varied between years. Remarkably, in that specific year (2014) when we detected the smallest magnitude of habitat differences in caterpillar biomass we also found the smallest habitat differences in breeding success (Seress et al. 2018). However, we have not explored yet how low caterpillar availability in the environment affects nestling diet and parental provisioning in these populations, which ultimately determines the influence of food limitation on the development and survival of nestlings in urban broods.

The aim of the present study was to compare the composition and the amount of nestling food between urban and forest habitats. To do this, we analysed video recordings of the parents' feeding behaviour in the two urban and two forest great tit populations (described in ***Chapter II***) and determined the prey type and volume of the food items brought to the nestlings. To make our results generalizable, we involved a large number of broods (153 broods and more than 3000 feeding events) and conducted the study over three breeding seasons (2014-2016) that showed marked between-year differences in both the biomass of canopy-dwelling caterpillars and the great tits' reproductive success (Seress et al. 2018). In urban compared to forest great tit broods, we predicted (i) a decreased proportion of caterpillars and increased proportions of other arthropods and/or non-arthropod (e.g. anthropogenic) food items in the nestling diet, (ii) smaller size of prey items provisioned (including both caterpillars and other food items), and (iii) a lower amount of food per nestling. Furthermore, we also predicted to find (iv) the smallest habitat difference in the composition and/or amount of nestling diet in the year (2014) when we detected the smallest habitat differences in both the caterpillar biomass (in tree canopies) and the birds' reproductive success (Seress et al. 2018).

4.2. Methods

The characteristic of the study sites and the detailed general field protocol are described in ***Chapter II***. In a nutshell, in three years (2014, 2015, and 2016) we collected one 60 minutes long video sample per brood to collect data on the composition and amount of nestling diet provided by the parents. In this study, video recordings started between 8:00 and 18:15 (mean ± SE, forest: 11:57 ± 00:14, urban: 12:28 ± 00:18) when nestlings were about 10 days old (range: 8-12 days, mean ± SE forest: 9.82 ± 0.11, urban: 10.02 ± 0.1; day of hatching = day 1). During the three study years, we collected video recordings for 153 broods (2014: 30 and 20; 2015: 20 and 27; 2016: 27 and 29 forest and urban broods, respectively).

4.2.1. Variables extracted from the video recordings

We included videos in our analyses only from the annually first broods where both parents took part in nestling provisioning (i.e. both parents appeared on the video or were observed at or captured on the nest later during the same breeding event). We regarded a brood as the first breeding attempt of a pair if it was initiated before the laying date of the earliest known second brood at that study site and year by an individually identifiable female that successfully raised her first brood (i.e. fledged at least one young). We excluded 12 (7.3%) video-recorded nests from the analyses where one of the parents was never observed. We collected detailed data from the video recordings using VLC Media player (v.2.2.0.; Free Software Foundation 1991) which allows slow-motion and frame-by-frame playback. We calculated six variables to describe the composition and amount of nestling food separately for each brood (Table IV.1).

Table IV.1. *Variables used in the study to characterise nestling diet and food provisioning by parent great tits. Data to calculate these variables were collected from 60 minutes long video recordings conducted at each nest. Sample sizes differ between variables due to lack of information on the type of data necessary for the calculations or because the calculation was restricted to a subset of the broods (see Methods for explanations).*

Variable	**Categories / Calculation**	**Sample size, forest vs. urban**
(1) Prey type*	caterpillar, other arthropod, non-arthropod	1198 vs. 1053 prey items
(2) Number of feeding visits	number of feeding visits during the 60-min recording	77 vs. 76 broods
(3) Feeding rate	$\frac{\text{number of feeding visits}}{\text{number of nestlings}}$	77 vs. 75 broods
(4) Average prey volume**	$\frac{\text{sum of the volume of measured prey items}}{\text{number of measured prey items}}$	49 vs. 43 broods
(5) Hourly prey volume	$\frac{\text{average prey volume} * \text{number of feeding visits}}{\text{number of nestlings}}$	49 vs. 42 broods
(6) Caterpillar volume	$\pi l(0.5w)^2$; l: caterpillar length, w: caterpillar width	855 vs. 568 caterpillars

* Feeding events with unidentified prey items (n=955, forest: 374, urban: 581 prey items) were excluded from the analyses

** Volume was calculated for all prey items using the same formula given for caterpillar volume

For each parental visit, we determined the (1) prey type, categorized as ‘caterpillar’, ‘other arthropod’ (e.g. spiders, mosquitos), ‘non-arthropod’ food item (mainly seeds). We categorized a prey item as ‘un-identified’ when it was not properly visible from the video recordings hence cannot be allocated to one of the above described three food type categories (either because the parent bird entered the nest box too fast or the prey item was ‘smashed’). For each brood, we determined the (2) number of feeding visits (both parents combined) during the 60-min observation and calculated (3) feeding rate, as the number of feeding visits divided by the number of living nestlings (counted before the recording) for each brood. To quantify the amount of nestling food we estimated prey volume for each prey item following and further developing the method described in ***Chapter III.*** In short, we took a screenshot of each feeding event when a parent bird held the prey item in front of the nest box's entrance hole (used as size reference) and measured the prey’s length and width digitally (Figure III.1) as well as calculated its volume (in mm^3) assuming they had the shape of a cylinder (Slagsvold and Wiebe 2007). In ***Chapter III,*** we showed that with this method we can accurately measure both prey length and width for approximately one-third of the prey items. However, in many of the remaining cases we were still able to estimate an approximate prey size relative to the birds' beak length and height. In this study, the data extrapolation method developed in ***Chapter III*** was refined, as follows. To estimate prey size in these cases, we first created four length (short, medium, long, and extra-long) and three width categories (thin, medium, and thick) based on prey length and width relative to beak length and height, respectively, and categorized the visible but non-measurable prey dimension into one of these length and/or width categories (Table A4.1). Then we also classified all those preys into the same categories for which size dimensions (i.e. length and width) were measured accurately (i.e. in mm; Table A4.1). From these latter, accurately measured length and width data, we calculated the mean for each of the four length and the three width categories (in mm; Average length and Average width columns in Table A4.1). Thus, using this procedure we were able to provide an estimate for the mean length or width for preys in each size categories, based on data of those subsets of preys in the categories that we were able to measure.

Finally, we also defined 12 volume categories as the combinations of the 4 length and 3 width categories (e.g. short × thin, short × medium, etc., Table A4.2). Using either the accurate size data (i.e. those measured in mm from screenshots) or the above-described size estimates for the length and width categories (Table A4.1), we calculated prey volume as follows:

a) When both length and width were accurately measurable for a prey item (in mm, from the screenshot) we calculated prey volume using the cylinder formula (see above).

b) If either the length or the width of the prey item was accurately measured but the other size parameter was only categorized, we assigned the category's average value for that missing size parameter (Table A4.1), and calculated prey volume using this estimated size. For example, if a prey item was 20 mm long and its width was categorised as 'thin', we used the 20 mm length and the average value of the 'thin' category (2.48 mm) to calculate prey volume by the cylinder formula.

c) Finally, when neither the length nor the width could be measured, but we could categorize both parameters relative to the beak size, we used the estimated average volume of the volume category (Table A4.2). For example, for a prey in the short × thin category, this was 27.77 mm^3 which is the average volume of this prey volume category.

In cases of (b) and (c), we used the average beak size (adult males and females combined) measured in our studied great tit populations (Sinkovics et al. 2018, unpublished data) as a size reference to define the upper and lower threshold of categories (there were no difference in beak sizes between the study populations, so we used the pooled average beak size). With the help of the above-described extrapolation method, we were able to estimate prey volume in 63.8 % of the prey items (62.5 % in urban, 65.3 % in forest broods), which proportion is similar to other studies investigating nestling diet (Grieco 2002).

From these prey volume estimates, we calculated the (4) average prey volume for each brood which refers to the volume of food delivered to the nest per feeding event. We also calculated the (5) hourly prey volume per nestling for each brood, by multiplying the average prey volume with the number of feeding visits and divided by the number of nestlings, which estimates the total amount of food that one nestling received during the 60-min observation. Finally, (6) individual caterpillar volume was also a separate variable, which we determined for each caterpillar specimen we were able to estimate from the videos (Table IV.1). We detected a total of 35 visits (1.2% of the total number of confirmed feeding visits) when parents entered the nest box without prey (called ‘prey-free’ visits) and excluded these from all calculations. Besides, there were 259 visits, when a parent bird moved so fast across the screen that we did not see whether it had any prey in its beak (‘uncertain events’). These uncertain events were counted as feeding events with ‘unidentified’ prey items because ‘prey-free’ visits were very rare.

4.2.2. Statistical analyses: the general scheme of modelling approach

All statistical analyses were conducted using R statistical software (R Core Team 2017) (version 3.4.3.) using the following packages: “nlme” (Pinheiro et al. 2017), “emmeans”(Lenth 2018), “MASS” (Venables and Ripley 2002), “car” (Fox and Weisberg 2011), and “multcomp”(Hothorn et al. 2008). To test our specific predictions for the effects of habitat and year on the composition and amount of nestling diet (see Introduction) we conducted pre-planned pairwise comparisons as suggested by Ruxton & Beauchamp (Ruxton and Beauchamp 2008). In general, our data analysis consisted of two main steps (Figure IV.1).

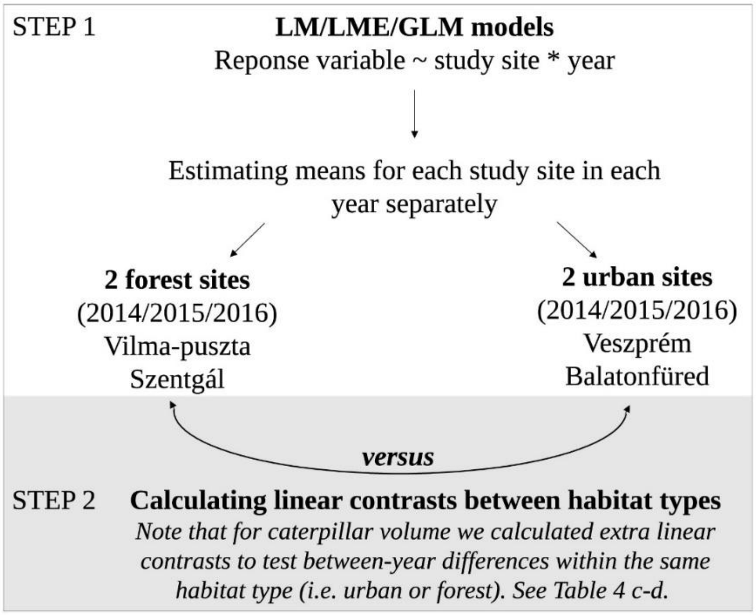


Figure IV.1. *Schematic illustration of the statistical analysis process. In Step 1, we built a separate statistical model for each dependent variable. In Step 2, we tested habitat (forest vs. urban) difference in the dependent variable using linear contrasts from the model built in Step 1.*

First, we constructed separate statistical models for each response variable. These models always included the study site (4 sites), year (3 years), and the study site × year interaction as predictor variables. We also tested the effects of the following potential confounding variables: ambient air temperature at the start of the observation, date, and time of the day at the start of the recording. Time of day was categorized as a three-level factor: between 8-11 h (n = 60 broods: 33 forest and 27 urban broods), 11-14 h (n = 59 broods: 31 forest and 28 urban broods), 14-18:15 h (n = 33 broods: 13 forest and 20 urban broods). Note that, because the onset of breeding season varied between years and sites, we mean-centered the date separately for each site and year combination, to express the relative dates of video recordings for each population within each year. This transformation reduced the multicollinearity of the date variable with year and site in the models and also controlled for possible seasonal effects in ‘early’ and ‘late’ first broods more precisely than the calendar date. Because none of these potential confounding variables had a significant effect in the models (see Tables A4.3-5 for the results of the extended models), in the second step of the analyses (pre-planned pairwise comparisons, see below) we used the results of models including only site, year, and site × year interaction.

Because for 12 pairs we had more than one video recordings (from two of the three years), for each response variable we also built linear-mixed-effect models using pair ID as a random factor (the models were otherwise identical to that described above). We then compared each model pair (i.e. with and without the random factor) using likelihood ratio tests to see which model has a better fit. We found no statistically detectable differences between the model pairs ($\Delta AIC \leq 2$ and $p > 0.779$) indicating that inclusion of pair ID as random effect did not improve model fit, so we ran our models without pair ID. The models we built for each specific response variable were as follows.

4.2.3. Analyses of the composition of nestling diet

To analyse the composition of the nestling diet we built generalized linear mixed models (GLMM) with binomial error distribution and "logit" link formula. We used brood ID as random factor to control for repeated feeding events by the same pair during 60-min. We built two models: the first model investigated the proportion of caterpillars in the nestling diet, thus, we used the proportion of caterpillars as the response variable (coded as: caterpillars = 1, all other identified food items = 0). In the second model, we investigated the composition of the non-caterpillar part of the nestling food, and the response variable was the proportion of other arthropods (spiders, etc; coded as: other arthropods = 1, non-arthropod prey items = 0). Note that in these two analyses we only included the identified prey items, i.e. we analysed only the identified fraction of the nestling diet (categorised as 'caterpillar', 'other arthropod', 'non-arthropod; n=2251; forest: 1198, urban: 1053 prey items), whereas the unidentified prey items were excluded from the models (n=955, forest: 374, urban: 581 prey items).

4.2.4. Analyses of the amount of nestling food

To investigate differences in the amount of nestling food, we built separate linear models for the following four response variables: number of feeding visits, feeding rate, average prey volume, and hourly prey volume. In the models of the number of feeding visits, we could include all observations (n = 153 broods: 77 forest and 76 urban broods). Three recordings were a few minutes shorter (with maximum 5 minutes), in these cases, we extended and calculated the number of feedings for 60 minutes. We had to exclude one urban brood from the feeding rate model due to missing information on brood size (Table IV.1). For average prey volume and hourly prey volume, we used only a subset of the observed broods (for average prey volume: n = 92 broods: 49 forest and 43 urban and broods, for hourly prey volume: n = 91 broods: 49 forest and 42 urban broods; Table IV.1.) which fulfilled the following two conditions: (1) we were able to estimate the volume of at least four prey items during the 60-min recording, and (2) at least 60 % of the prey items had volume estimations. We used these two criteria because for some nests we were able to determine prey volume only for a small fraction of prey items, so the estimation of the average and hourly prey volumes would have been highly uncertain and/or biased in such cases. We tested several other thresholds for these inclusion criteria (minimum 4 prey volume estimation and at least 50%, 60%, 70%, 80% of prey items had volume estimation, or minimum 6 prey volume estimation and at least 50%, 60%, 70%, 80% of prey items had volume estimation) but the direction and magnitude of the site/habitat/year differences were not influenced by applying stricter conditions (which, however, resulted in much more reduced sample sizes). Thus we chose the above thresholds because those provided a balance between reducing uncertainty and still allowing the use of appropriate sample sizes for statistical analyses.

To investigate differences in caterpillar volume between study sites and years, we built a linear mixed-effect model (LME) where the response variable was caterpillar volume (i.e. estimated volume of individual caterpillars, n = 1423, Table IV.1). We included the brood ID as a random factor because several caterpillars from the same 60-min-observations were included. We applied the cube root transformation to caterpillar volume to meet the assumptions of the models.

4.2.5. Comparisons between urban and forest habitats and among years

In the second step of the analyses (Figure IV.1), we conducted pre-planned pairwise comparisons to test our specific predictions for the effects of habitat and year on the composition and amount of nestling diet. To do this, we calculated marginal means from the models described above for each of our study sites in each year using “emmeans” package (Lenth 2018). Then, we compared the two habitat types by calculating and testing the difference of these marginal means between the two forest sites versus the two urban sites for each year (Figure IV.1). All these differences were derived from the parameters and associated errors estimated by each model as linear contrasts of least-squares means (Lenth 2018). For the LME model of caterpillar volume, we calculated two additional sets of linear contrasts as follows: (1) between-year comparisons within the forest habitat and (2) between-year comparisons within the urban habitat (i.e. 2014 vs. 2015, 2014 vs. 2016 and 2015 vs, 2016 for both habitats). Please note that a significant site effect (or site × year interaction) detected in the linear models does not necessarily result in a significant habitat effect (or different habitat effects in different years) in the contrast analyses because these effects may be inconsistent between the two sites in the same habitat. Conversely, weak and non-significant site effects (or its yearly variation) can produce a detectable difference in the habitat comparisons.

We used this linear contrast approach rather than including habitat type as a fixed effect and site as a random effect in the models because variance estimations of random effects with few levels (only four in our case) are unreliable (Bolker et al. 2009; Vincze et al. 2019). We applied the false discovery rate (FDR) method for correcting *P*-values for multiple comparisons. We checked the statistical assumptions for each model by visually examining their residual plots (Zuur et al. 2009; see Appendices for the diagnostic figures for each final model; Figure A4.1.). We define the statistical significance level at 0.05 and refer to results where $0.05 < P < 0.1$ as marginally non-significant.

4.3. Results

4.3.1. Composition of nestling diet

In total, we recorded 3206 feeding events and were able to assign 2251 prey items into the three analysed prey type categories (caterpillar, other arthropod, non-arthropod). The proportion of caterpillars in the nestling diet showed significant differences between study sites and we also found a significant site × year interaction (Table IV.2A). The linear contrasts indicated that, in each year, forest great tit nestlings received a higher proportion of caterpillars than urban ones, although in 2015 the habitat difference was marginally non-significant (forest vs. urban: 2014: 89 % vs. 69.2%; 2015: 83.4% vs. 69.8%; 2016: 89.3% vs. 56.4%; Figure IV.2, Table IV.2B). In the case of the non-caterpillar fraction of the nestling food, we found that the proportions of the two food categories (i.e. other arthropod prey vs. non-arthropod prey) differed both between sites and years, although the site × year interaction was not significant (Figure IV.2., Table IV.2A). The linear contrasts indicated that in 2015 and 2016 urban nestlings received lower proportions of non-caterpillar arthropods compared to forest nestlings, but we found no such habitat difference in 2014 (Figure IV.2. Table IV. 2B).

Table IV.2. *Comparisons of the composition of nestling diet between sites, habitats, and years. (A) GLM models and the (B) linear contrasts between habitats (forest compared to urban habitat for each year; positive estimates indicate higher values in the forest). Statistically significant ($p < 0.05$) differences are highlighted in bold. For linear contrasts, p-values were adjusted using the false discovery rate (FDR) method. Please note that the rows are for different information in parts (A) and (B).*

	(A) GLM models			**(B) Linear contrasts between urban and forest habitats in each year**		
Predictors	**DF**	**$\chi2$**	**p-value**	**year**	**contrast ± SE**	**adjusted p-value**
Caterpillar vs. non-caterpillar						
Site	3	72.579	**< 0.001**	2014	1.099 ± 0.323	**0.001**
Year	2	1.831	0.400	2015	0.623 ± 0.319	0.053
Site × Year	6	16.536	**0.011**	2016	1.695 ± 0.290	**< 0.001**
Other arthropods vs. non-arthropods						
Site	3	21.455	**< 0.001**	2014	0.928 ± 0.694	0.184
Year	2	7.033	**0.030**	2015	2.528 ± 0.635	**< 0.001**
Site × Year	6	9.447	0.150	2016	1.470 ± 0.565	**0.016**

Sample sizes (number of identified prey items, forest vs. urban):
Caterpillar vs. non-caterpillar: 2014: 534 vs. 279; 2015: 289 vs. 398; 2016: 375 vs. 376
Other arthropods vs. non-arthropods: 2014: 59 vs. 86; 2015: 48 vs. 120; 2016: 40 vs. 164

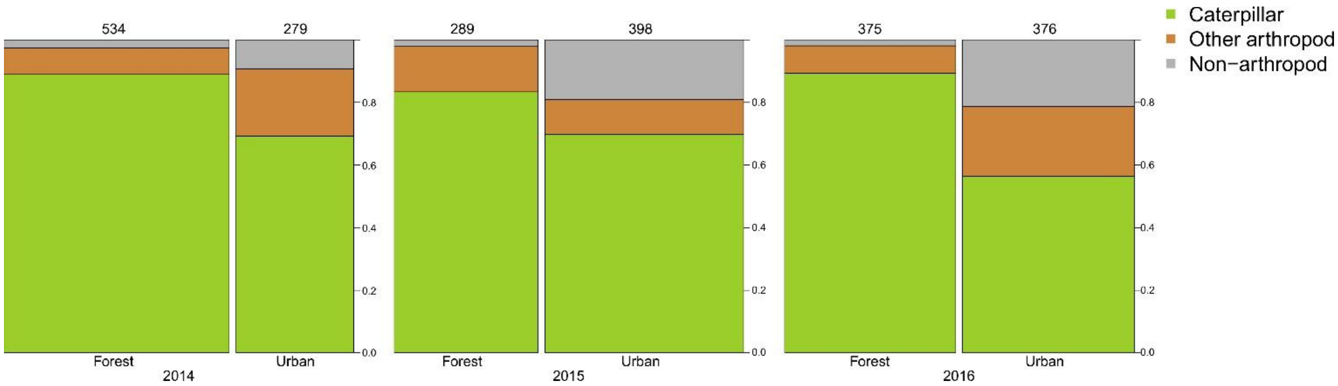


Figure IV.2. *Proportions of different prey types (caterpillar, other arthropod, and non-arthropod) provisioned to great tit nestlings for each year and habitat type. The numbers of identified prey items are indicated above each column and are proportional to the width of the columns.*

4.3.2. Amount of nestling food

The total number of the parents' feeding visits during the 60-min observations significantly differed between sites, but the site × year interaction was non-significant (Table IV.3A). Linear contrasts did not indicate a consistent habitat difference, meaning that on average urban parents visited their nests as frequently as forest parents in all years (Table IV.3B, Figure IV.3A). However, when we compared feeding rates (i.e. the number of feeding visits per nestling) the linear model showed a significant effect for the site and also for the site × year interaction (Table IV.3A). The results of habitat contrasts showed higher feeding rates per nestlings for urban broods in 2015 and 2016 (Table IV.3B, Figure IV.3B), but not in 2014.

Regarding the average prey volume, we also found significant site and year effects, but the site × year interaction was not significant (Table IV.3A). Linear contrasts between habitats showed that in 2015 and 2016 urban parents brought smaller prey items per feeding visit than their forest conspecifics (Table IV.3B, Figure IV.3C), whereas in 2014 the habitat difference was not significant. For hourly prey volume (i.e. the total amount of food that a nestling received during the 60-min observation), we found a significant site × year interaction (Table IV.3A). However, the habitat contrasts calculated from this model did not indicate significant habitat differences: on average urban and forest nestlings received the same amount of food during the observation period in all three years (Table IV.3B, Figure IV.3D).

Table IV.3. *Comparison of feeding visits, feeding rates, and prey volumes between habitats. Results of (A) LM models and the (B) derived linear contrasts (forest compared to urban habitat for each year; positive estimates indicate higher values in the forest) in the number of feeding visits (number/hour), feeding rate (number/nestling/hour), average prey volume (mm^3/feeding visit), and hourly prey volume (mm^3/nestling/hour). Statistically significant ($p < 0.05$) differences are highlighted in bold. For linear contrasts, p-values were adjusted using the false discovery rate (FDR) method. Please note that the rows are for different information in parts (A) and (B).*

	(A) LM models			**(B) Linear contrasts between urban and forest habitats in each year**			
Predictors	**DF**	**χ2**	**p-value**	**year**	**contrast ± SE**	**t**	**adjusted p-value**
Number of feeding visits							
Site	3	1721.2	**0.001**	2014	- 0.592 ± 3.228	-0.183	0.855
Year	2	139.1	0.517	2015	- 4.171 ± 3.292	-1.267	0.311
Site × Year	6	863.4	0.231	2016	- 5.027 ± 2.806	-1.791	0.226
Feeding rate							
Site	3	41.033	**< 0.001**	2014	- 0.312 ± 0.357	- 0.875	0.383
Year	2	5.388	0.126	2015	- 1.145 ± 0.364	- 3.149	**0.003**
Site × Year	6	16.950	**0.046**	2016	- 1.501 ± 0.315	- 4.772	**< 0.001**
Average prey volume (mm^3)							
Site	3	74677	**< 0.001**	2014	7.793 ± 24.623	0.317	0.752
Year	2	69126	**< 0.001**	2015	59.331 ± 23.876	2.485	**0.023**
Site × Year	6	32212	0.225	2016	92.924 ± 23.701	3.921	**< 0.001**
Hourly prey volume (mm^3)							
Site	3	137041	0.103	2014	- 40.627 ± 58.233	- 0.698	0.723
Year	2	106500	0.090	2015	- 70.758 ± 56.467	- 1.253	0.642
Site ×Year	6	331497	**0.025**	2016	21.278 ± 59.906	0.355	0.723

Sample sizes (number of broods, forest vs. urban):
Number of feeding visits: 2014: 30 vs. 20; 2015: 20 vs. 27; 2016: 27 vs. 29
Feeding rate: 2014: 30 vs. 20; 2015: 20 vs. 27; 2016: 27 vs. 28
Average prey volume: 2014: 17 vs. 12; 2015: 15 vs. 17; 2016: 17 vs. 14
Hourly prey volume: 2014: 17 vs. 12; 2015: 15 vs. 17; 2016: 17 vs. 13

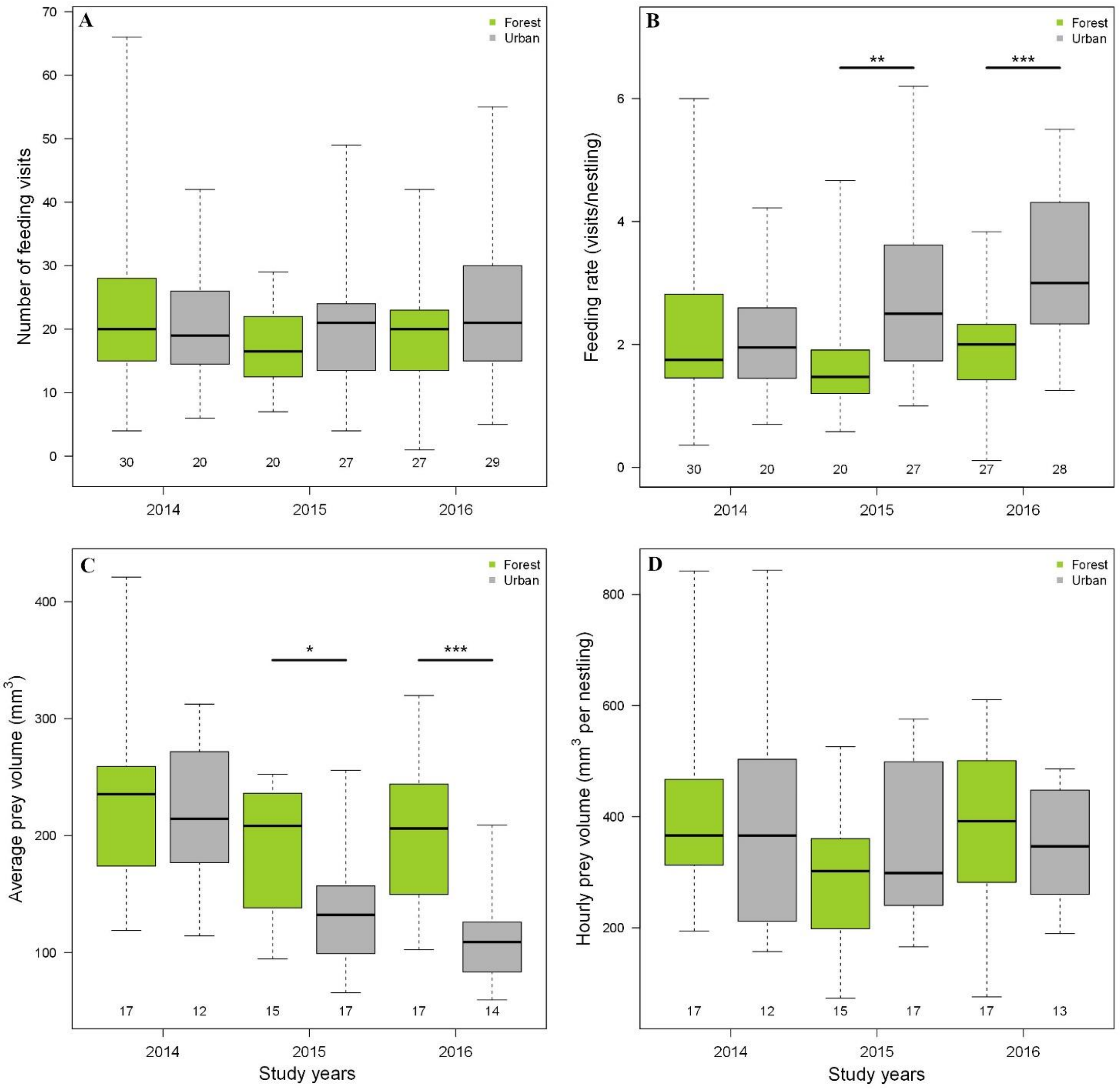


__Figure IV.3.__ The amount of food provisioned to great tit nestlings during 60-min video observations in forest and urban habitats in the three years of the study. (A) Number of feeding visits of great tit parents (number/hour, both parents combined). (B) Feeding rate of parents per nestlings (number/nestling/hour). (C) Average prey volume delivered by the parents to nestlings (mm^3/feeding visit). (D) Hourly prey volume per nestling, that estimates the total amount of food that one nestling received during the observation (mm^3/nestling/hour). Boxes show the interquartile range, the thick line is the median, and whiskers refer to the range of data distribution. Sample sizes (number of broods) are indicated below each group. Statistically significant differences between the performance of forest and urban parents in a given year are marked with asterisks (: $p \leq 0.05$, **:$p \leq 0.01$, *** $p \leq 0.001$)*

For caterpillar volume, we found significant site and year effects and the site × year interaction was also significant (Table IV.4A). The linear contrasts testing the habitat difference revealed that in 2015 and 2016 urban parents delivered smaller caterpillars to their nestlings than forest parents (Table IV.4B, Figure IV.4), whereas there was no difference in 2014 (Table IV.4B, Figure IV.4). Within the urban habitat, linear contrasts showed a significant between-year variation: caterpillars delivered to urban nestlings were significantly larger in 2014 than either in 2015 or 2016 (Table IV.4C, Figure IV.4), and in 2015 they were also larger than in 2016 (Table IV.4C). In contrast, we found no annual difference in caterpillar size in the forest habitat (Table IV.4D, Figure IV.4).

Table IV.4. *Habitat and annual differences in caterpillar volume in the diet of great tit nestlings. Results of the (A) LME models and the (B-C-D) derived linear contrasts. Section (B) shows the habitat contrasts in caterpillar volume for each year, positive estimates indicating higher values in the forest. Sections (C) and (D) show annual differences in urban and forest caterpillar volume, positive estimates indicating higher values in the first year of the comparison. Statistically significant ($p < 0.05$) differences are highlighted in bold. For linear contrasts, p-values were adjusted by the false discovery rate (FDR) method.*

	(A) LME model		
	DF	**$\chi2$**	**p-value**
Caterpillar volume			
Site	3	22.906	**< 0.001**
Year	2	29.180	**< 0.001**
Site × Year	6	21.847	**0.001**

(B) Habitat difference in caterpillar volume (linear contrast)			
year	**contrast ± SE**	**t**	**adjusted p-value**
2014	-0.201 ± 0.262	-0.766	0.445
2015	0.730 ± 0.265	2.257	**0.010**
2016	1.203 ± 0.236	5.105	**< 0.001**

(C) Annual difference in urban caterpillars' volume (linear contrast)			
year	**contrast ± SE**	**t**	**adjusted p-value**
2014-2015	1.150 ± 0.270	4.265	**< 0.001**
2014-2016	1.734 ± 0.263	6.589	**< 0.001**
2015-2016	0.584 ± 0.252	2.312	**0.022**

(D) Annual difference in forest caterpillars' volume (linear contrast)			
year	**contrast ± SE**	**t**	**adjusted p-value**
2014-2015	0.220 ± 0.257	0.856	0.591
2014-2016	0.331 ± 0.234	1.415	0.478
2015-2016	0.111 ± 0.249	0.447	0.655

Sample sizes (number of caterpillars, forest vs. urban):
2014: 361 vs. 159; 2015: 201 vs. 230; 2016: 293 vs. 179

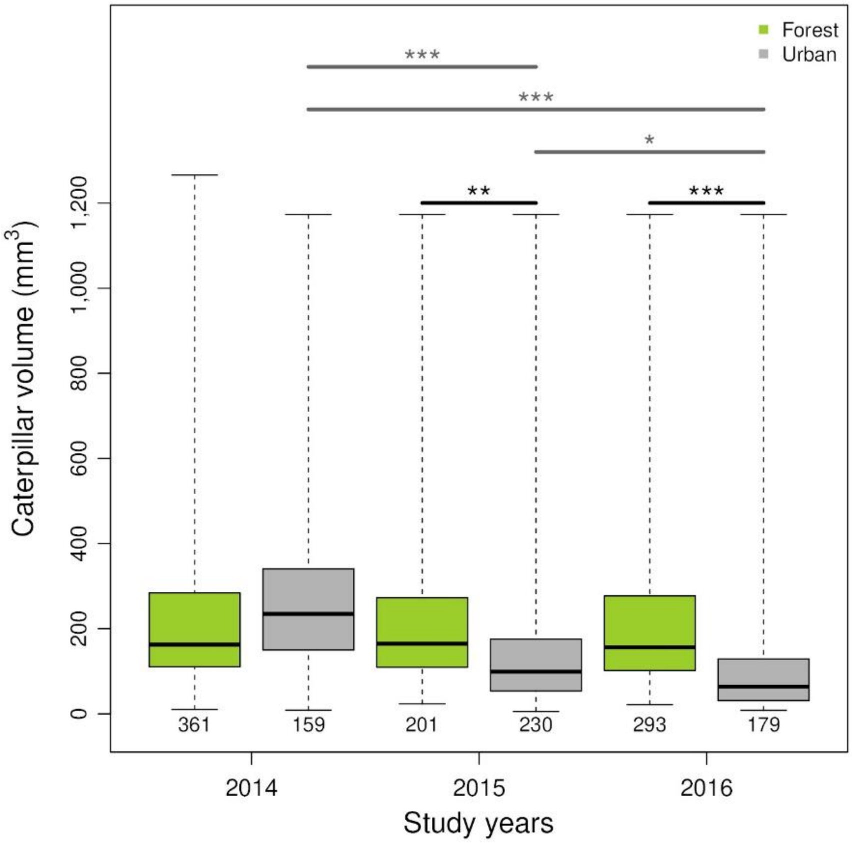


Figure IV.4. *The volume of caterpillars provisioned to great tit nestlings in forest and urban habitats in the three years of the study. Sample sizes are indicated below each group. Boxes show the interquartile range, the thick line is the median, and whiskers refer to the range of data distribution. Statistically significant differences between habitats (black horizontal lines above the boxes) and years (grey horizontal lines above the boxes) are marked with asterisks (*: $p \leq 0.05$, **:$p \leq 0.01$, *** $p \leq 0.001$).*

4.4. Discussion

Our results support, at least in some years, our initial predictions that (i) great tit nestlings in urban broods receive decreased proportions of caterpillars but increased proportions of non-arthropod food items (e.g. seeds), and that (ii) urban nestlings receive smaller prey items than nestlings in forest broods. However, our results did not support the prediction that (iii) urban nestlings receive a lower amount of food *per capita* because urban parents fed their nestlings more often relative to forest parents, which compensated for the smaller size of the prey items. Finally, as we expected (prediction iv), we found the smallest – and mostly non-significant – habitat difference in nestling diet in 2014 when the differences both in caterpillar biomass and in breeding success were also the smallest between urban and forest habitats

(Seress et al. 2018). Collectively, these results support the hypothesis that the shortage of optimal nestling food is an important limiting factor for the reproductive success of urban great tits (Seress and Liker 2015; Bailly et al. 2016; Seress et al. 2018, 2020), similarly to those natural forest types that also have low caterpillar abundance (Tremblay et al. 2005; Serrano-Davies and Sanz 2017). Besides, our study provided novel evidence on the particular importance of food quality and highlighted remarkable annual variation in the level of high-quality food in urban environments.

Nestling diet and reproductive success in 'bad caterpillar' years in urban habitat

In two of the studied years (2015, 2016), both the biomass of arboreal caterpillars and the breeding success of great tits were much lower in urban compared to forest habitats (Seress et al. 2018). In these two years, caterpillars dominated the diet of forest nestlings (80-90%), whereas their proportion was much lower in urban nestlings' food palette (50-70%). Urban parents compensated for the shortage of caterpillars by provisioning more non-arthropod food items (e.g. seeds, anthropogenic food) to their offspring. Despite having smaller broods, urban parents had to take a feeding effort (reflected by the total number of feeding visits per hour) similar to forest parents to provide a similar amount of food per offspring, due to the smaller size of prey items they could deliver. Thus, these results demonstrate that urban great tit parents are capable of quantitatively compensating for the low amount of food available in their environment by (1) taking care of broods of fewer offspring and (2) increasing their feeding effort per nestling.

Nevertheless, urban birds had much more reduced reproductive success in these years: they not only produced fewer fledglings (the mean habitat difference was 5.4 and 5.0 fledglings in 2015 and 2016, respectively), but the fledglings had also c. 20% lower body mass in urban compared to forest broods (on average by 3.4 and 3.3 g per nestling in 2015 and 2016, respectively; see Table 3 in Seress et al. 2018). Furthermore, Seress et. al (2018) also found that urban broods suffered from significantly higher starvation-related nestling mortality than forests broods. Thus, the above results on nestling body mass and survival indicate that even if urban parents can provide the same quantity of food per nestling, the unfavourable composition of nestling diet can clearly limit nestling development and survival in cities.

There are relatively few studies that examined both the composition and amount of nestling diet in relation to urbanization. Two recent comprehensive studies conducted in the same populations of blue tits in Scotland partially support our conclusions. In line with our results, these studies found that urban nestlings received smaller proportions of caterpillars and the size of the caterpillars was smaller compared to the forest (Pollock et al. 2017; Jarrett et al. 2020). The feeding rate was almost twice as high in urban than in the forest broods in one study (Pollock et al. 2017), although it did not differ between the habitats in the other (Jarrett et al. 2020). The overall conclusions of these studies were in line with ours: the low-quality nestling diet (lack of caterpillars) is responsible for the lower body mass of nestlings in urban broods (Pollock et al. 2017; Jarrett et al. 2020). Senar et al. (2021) also found that urban great tit nestlings received lower proportions of caterpillars, which was presumably the reason for the reduced breeding success in urban areas. However, they reported lower feeding rates in an urban habitat, although did not find habitat differences in the size of prey (Senar et al. 2021). Mennechez and Clergeau (2006) found that in the common starling food volume received by the nestlings was reduced (cc. by 50%) in the urban centre compared to the periurban and suburban areas, and the composition of nestling food was also unfavourable in the urban centre (contained more human refuse; Mennechez and Clergeau 2006). Several other studies that investigated only a single aspect of nestling food (i.e. either its composition or its quantity) similarly concluded that the low-quality nestling diet and/or the lower amount of nestling food is responsible for the reduced breeding success in urban habitats both in tit species (Riddington and Gosler 1995; Sinkovics 2014; Narango et al. 2018; de Satgé et al. 2019; Corsini et al. 2021) and in other birds (Mennechez and Clergeau 2001; Shawkey et al. 2004; Newhouse et al. 2008; Heiss et al. 2009; Seress et al. 2012; Meyrier et al. 2017; Baldan and Ouyang 2020).

Nestling diet and reproductive success in a 'good caterpillar' year in urban habitat

In 2014 we found a much smaller habitat difference in nestling diet than in the other two years. Although urban nestlings received fewer caterpillars than forest nestlings, the non-caterpillar fraction of their food contained more other arthropods rather than non-arthropod food, similarly to the forest habitat. Furthermore, we did not find significant habitat differences in the amount of the nestling food: neither the hourly number of feeding visits and the feeding rate nor the average prey volume and hourly prey volume per nestling differed between the habitat types. In parallel with these results, the habitat differences in breeding success were also smaller than in the other two years (1.4 fledglings, and 1.6 g in their body mass; see Table 3 in Seress et al. 2018).

Our results on the annual changes in caterpillar size may provide a likely explanation for the reduced habitat difference in nestling diet and breeding success in 2014. This year urban pairs delivered much larger (2.2 times larger on average, calculated from raw data) caterpillars compared to the other two years, and similar in size to the caterpillars provisioned in the forest. Thus, urban parents were probably able to provide enough high-quality food for their nestlings, which resulted in improved nestling development. The importance of large prey items in the nestling diet was also reported in earlier studies. For example, Schwagmeyer & Mock estimated that a single large (>2 cm) prey item's dry weight is 30–40 times greater than that of a small one (< 0.6 cm). They also showed that the delivery rate of these large prey items (called 'e-preys') strongly predicted fledgling body mass and recruitment in house sparrows (Schwagmeyer and Mock 2008).

It is not entirely clear why urban great tits could feed their young with larger caterpillars in 2014 than in the other two years. One possible explanation is that the unusually warm spring of 2014 (see Figure S2 in Seress et al. 2018) favoured the growth of caterpillars in the cities, as temperature can affect their feeding activity (Kingsolver and Woods 1997). Our estimates for canopy caterpillar biomass do not support this explanation, however, because we did not detect increased caterpillar biomass in urban trees that year (Seress et al. 2018). However, we did not monitor all tree species in our study sites, thus it is possible that large caterpillars represented moth species that developed on unmonitored but common tree species in our urban study sites. Similarly, we did not monitor caterpillars on other components of the vegetation including understory shrubs and grassy areas. In cities we often saw tits feeding on or searching for food on the ground or in the bushes, thus the increased caterpillar size in their diet may be due to the appearance and/or gradation of moth species that developed in these types of vegetation and reached large body size in 2014.

Conclusions

In general, our results suggest that urban great tits are capable of delivering similar amounts of food per nestling as forest great tits due to the smaller brood size and because they feed their offspring relatively more often (compensating for the smaller amount of food per feeding event) than parents do in forests. Despite this, the size and survival of urban nestlings usually cannot reach the levels found in forest broods due to the lower quality nestling food (fewer and smaller caterpillars as well as increased proportions of non-arthropod food in the diet). However, our results from 2014 suggest that sometimes it is possible to catch a better year in the city when urban parents can feed their offspring with large caterpillars and relatively more other arthropods, which probably caused the detectable increase in urban birds' reproductive success in that year. The crucial effect of the arthropod component of the nestling food was also supported experimentally in our study system: the provisioning of extra mealworms to urban nestlings during the chick-rearing period resulted in substantially larger body size and higher survival rates that were similar to their unsupplemented conspecifics in a forest habitat (Seress et al. 2020).

Finally, our study clearly demonstrates that long-term studies on urban populations with robust sample sizes are needed to fully understand the implications of among-year variation in environmental conditions. Our results suggest that caterpillar size, which is likely an important determinant of nestling diet quality, varies significantly among years in the cities, and this variation appears larger than in the forest (at least in the three years we studied). If data are based on only one year of observations and small sample sizes, the generalizability of the results can be very limited due to the strong annual variations (Cholewa and Wesołowski 2011) like the one we reported for the nestling diet in this study.

CHAPTER V

COMPARISON OF NESTLING DIET BETWEEN FIRST AND SECOND BROODS OF GREAT TITS *(PARUS MAJOR)* IN URBAN AND FOREST HABITATS

Csenge Sinkovics, Gábor Seress, Ivett Pipoly, Ernő Vincze & András Liker

Abstract

To understand why early broods tend to be more successful than late broods we investigated the nestling diet and reproductive success of great tit pairs that had both a first and a second brood in the same breeding season. We found that in forest habitats great tit parents delivered similar composition and amount of food per nestlings throughout the breeding season, resulting in similar nestling body mass and survival in both first and second broods. In urban habitats, however, although parents provided similar amounts of food to the second broods but they tended to deliver fewer caterpillars. In parallel with this, we observed lower nestling survival in second urban broods than in first broods even though the body mass of surviving nestlings was similar to that of the first broods. These findings suggest that although parents produce smaller second broods in both habitats, they are able to compensate for lower food availability in forest habitats but not in urban habitats, thus leading to reduced food quality and lower offspring survival in urban second broods.

This chapter is an extended version of the research article „Csenge Sinkovics, Gábor Seress, Ivett Pipoly, Ernő Vincze & András Liker (2023): Comparison of nestling diet between first and second broods of great tits *Parus major* in urban and forest habitats. *Animal Biodiversity and Conservation 46.2: 199-212*”.

5.1. Introduction

Seasonal declines in reproductive performance have been observed in a wide variety of avian taxa (Price et al 1988, Perrins and McCleery 1989). For example, clutch size (Hochachka 1990, Mägi and Mänd 2004, Kaliński et al 2009, Winkler et al 2020), number of fledglings (Stodola et al 2009, Winkler et al 2020, Bukor et al 2021), fledging success (Mägi and Mänd, 2004; Öberg et al 2014), nestling mass/growth rate (Sedinger and Flint 1991, Jensen et al 2023), and recruitment (Hochachka 1990, Lambrechts et al 2008) often decrease with a later hatch date within the reproductive season. Two main hypotheses have been proposed to explain why early breeders are more successful than late breeders (Verhulst and Nilsson 2008). The parental quality hypothesis proposes that the seasonal decrease in reproductive success is caused by changes in the parents' phenotype. Individuals with higher phenotypic quality (for example, in better condition; Wendeln and Becker 1999) may reproduce at the start of the breeding season while lower quality pairs may reproduce later. This difference in parents’ phenotype can result in a negative correlation between breeding time and breeding success. This idea has been supported, for example, by an experimental study by De Neve et al (2004) that compared the breeding success of first clutches (reared by foster parents) with induced replacement clutches of the same magpie *(Pica pica)* pairs. They found that breeding success of the pairs' replacement clutches was similar to that of their first clutches (reared by foster parents), and that some components of the breeding success of the replacement clutches were significantly higher than that for late-season first clutches of other magpie pairs. They concluded that within-individual variation cannot explain the seasonal variation, and therefore among-individual variation in parental quality is a more likely explanation for differences between early breeders and late breeders in magpies.

According to the date hypothesis, seasonal changes in the environment (such as food availability) are the primary cause of this negative trend. As introduced in ***Chapter I***, many insectivorous birds, especially passerines, rely on caterpillars in their nestling rearing period (Krištín and Patočka 1997, Sinkovics et al 2021)., however, the abundance of caterpillars often shows strong seasonal patterns. In early spring caterpillar larvae are highly abundant (called ‘caterpillar peak’) while later in the season their biomass strongly decreases (Seress et al 2018, Laczi et al 2019, Smith and Smith 2019, Nadolski et al 2021). Several studies have highlighted the connection between caterpillar abundance and avian breeding success. Verboven et al (2001), for example, found that both clutch size and success of the first clutch were positively related to caterpillar density in individual territories, while Nagy and Holmes (2005) found that food availability was a strong predictor of double brooding of black-throated blue warblers *(Setophaga caerulescens).* An experimental study on tree swallows *(Tachycineta bicolor)* found that nestlings in delayed hatching nests had poorer body condition and weighed less than their non-delayed counterparts, and it was suggested this could be due to the lower biomass of available insects (Harriman et al 2017). As a consequence, according to the date hypothesis, nestlings hatched later in the season may develop in suboptimal food availability conditions, leading to their undernourishment and ultimately lower fledging success (Burger et al 2012, Kaliński et al 2019).

These two hypotheses are most likely non-mutually exclusive, and hatching date manipulation (that is, forcing females to lay a replacement clutch in order to delay their breeding time) is a frequently used method to experimentally investigate their relative importance (Verhulst et al 1995, Wardrop and Ydenberg 2003, De Neve et al 2004, García-Navas and Sanz 2011). Most such experimental studies support both hypotheses even within the same study (Arnold et al 2004). For example, Verhulst et al (1995) concluded that 80-90% of the seasonal decline in reproductive success of great tits *(Parus major)* could be explained by environmental effects (i.e., by the date hypothesis), and the remaining 10-20% of decline would be due to differences in quality between the parents of early and late breeders. Moreover, some authors found temporal variation in the relative importance of the two processes. For example, Wardrop and Ydenberg (2003) found that in tree swallows the date hypothesis better explained the decline in nestling mass in the first half of the season, while the parent quality hypothesis better explained the second half.

In this study, our aim was to test predictions of the date hypothesis by analysing the nestling diet of the same great tit pairs that had both first and second broods within the same breeding season. Although this approach is less common, it could provide valuable information on the temporal changes in parental behaviour and/or nestling diet without further disturbing the nest, an inherent feature of nest manipulation experiments. The great tit is an ideal candidate species for this study because it often breeds twice a year in our study region and breeding success and nestling condition typically differ significantly between first and second broods (Dubiec and Cichoñ 2001, Pimentel and Nilsson 2007, Bukor et al 2021). We examined nestling diet in two habitats at two forest study sites, and at two urban study sites (described in ***Chapter II***) that differed markedly in food availability. As shown in ***Chapter I (subsection 1.3.)***, we found that the average caterpillar biomass during the birds' breeding season was 2–12 times higher (depending on the study year) in the forest than in the urban study sites (Seress et al 2018). Additionally, the forest habitats were characterized by a single large caterpillar biomass peak during the nestling rearing period of the first broods (around May), and this biomass decreased greatly until the breeding season ended. In the urban study sites, we also observed a seasonal decline in caterpillars in some, but not all, years and sites, and the decline was less pronounced because urban trees showed several small caterpillar peaks throughout the breeding season (see Figure S3 in Seress et al 2018).

Because of this seasonal decline in food availability, we predicted changes in the amount and/or composition of the nestling diet and also a decrease in reproductive success. We selected 32 great tit pairs (10 forest, 22 urban pairs) that had two broods within the same breeding season and compared parental provisioning behaviour, nestling food composition, and breeding success between their annual first and second broods. Using video recordings of parental food deliveries, we determined the type and volume of individual food items brought to the nest. We predicted that the second broods in both habitats (1) would receive fewer caterpillars and higher proportions of other arthropods and/or non-arthropod (e.g., seeds) food items. We also predicted a lesser amount of nestling food in second broods than in first broods as the result of either (2) a lower feeding rate and/or (3) the delivery of smaller prey items. Due to the importance of large caterpillars for high fledging body mass and subsequent recruitment (Schwagmeyer and Mock 2008, Seress et al 2012, Sinkovics et al 2021), we also examined whether (4) the size of individual caterpillars delivered to the nest varied between first and second broods. Regarding breeding success, we predicted that second broods in both habitats would have lower (5) maximum brood size, (6) lower nestling body mass, and (7) lower nestling survival.

5.2. Materials and methods

The characteristic of the study sites and the detailed general field protocol are described in ***Chapter II***. In a nutshell, in three years (2014, 2015, and 2016) we analysed the provisioning behaviour of individually identified pairs (i.e., both parents had coloured-rings) who had successfully raised both their first and second broods during a breeding season (with a minimum of one young fledged in each brood). Median hatching date and range of the observed nests are shown in Table A5.1). In this study, video recordings started between 8:39 and 17:05 (hh:mm, mean ± SE, first vs. second broods, forest: 13:12 ± 00:40 vs. 11:44 ± 00:29, urban: 12:20 ± 00:30 vs. 11:46 ± 00:27) when nestlings were about 10 days old (range: 9-12 days, mean ± SE, age of first vs. second broods, forest: 9.6 ± 0.2 vs. 9.4 ± 0.2 days, urban: 9.96 ± 0.2 vs 9.79 ± 0.2 days; hatching day of the first nestling = day 1). We collected observations for both brood types (i.e., first and second) for 32 pairs (10 forest and 22 urban), resulting in a total of 64 video samples (Table A5.1).

5.2.1. Video analyses and the studied variables

From the videos, we collected four variables to estimate the composition and amount of food provided to nestlings (summarised in Table V.1A) using methods we developed in earlier studies (***Chapter III and IV***, Sinkovics et al 2018, 2021).

Table V.1. *The studied variables used to describe nestling diet and breeding success in the first and second broods of great tits. The table also shows the explanatory variables and random effects included in the initial models (i.e., step 1 in statistical analyses, see Methods for details). Two of the studied variables (non-caterpillar fraction of nestling diet and nestling survival) were analysed with Fisher's exact test/paired t-test (see text for justifications). Food data were collected from 60-min video recordings.*

		Statistical models	
Variable	**Categories/calculation**	**Explanatory variables**	**Random factors**
A) Nestling food variables			
(1) Prey type	caterpillar, other arthropod, non-arthropod, unidentified	1/a. Caterpillar vs. non caterpillar: Study site, Brood type, Year, Date of observation, Time of the day	Pair ID, Brood ID
		1/b. Non-caterpillar fraction: - (Analysed with Fisher's exact test)	
(2) Feeding rate	$\frac{\text{number of feeding visits per 60 min}}{\text{number of nestlings}}$	Study site, Brood type, Year, Date of observation, Time of the day	Pair ID
(3) Average prey volume*	$\frac{\text{sum of the volume of measured prey items}}{\text{number of measured prey items}}$		Pair ID
(4) Caterpillar volume	$\pi l(0.5w)^2$; l: length, w: mean width		Pair ID, Brood ID
B) Reproductive success variables			
(5) Maximum brood size	maximum number of eggs minus the number of unhatched/broken eggs	Study site, Brood type, Year	Pair ID
(6) Nestlings' body mass		Study site, Brood type, Year, Nestling age	Pair ID, Brood ID
(7) Nestling survival	$\frac{number\ of\ ringed\ nestlings}{maximum\ brood\ size}$	- (Analysed using paired t-test)	

From the video recordings we categorised the prey items delivered for each feeding visit into three prey types: caterpillars, other arthropods (e.g., spiders, mosquitos), and non-arthropod food items (e.g., seeds). We recorded a total of 953 parental nest visits and we were able to classify 594 prey items into the three prey type categories (Table V.2). Prey items that were not clearly visible (for example if the parent bird entered the nest box too fast) were classified as 'unidentified', and were included only in a subset of analyses (detailed below). Additionally, on 92 occasions, parent birds entered the nest box so fast that we were unable to determine the presence or absence of a prey item. We considered these 'uncertain events' as feeding events with 'unidentified' prey items because visits without prey items were very rare. We recorded only 15 prey-free visits, which is 1.8 % of the total number of confirmed feeding visits. Nest-visits without prey items were excluded from all calculations.

Table V.2. *Sample sizes of identified prey types and measured prey items in first and second broods within urban and forest habitats. Food data were collected from 60-min video recordings.*

	Forest		**Urban**	
	First	**Second**	**First**	**Second**
Prey type	**206**	**113**	**408**	**226**
Caterpillar	116	70	133	62
Other arthropod	13	12	45	71
Non-arthropod	1	1	60	10
Unidentified	46	22	116	68
Uncertain events	30	7	47	8
Prey-free visits	0	1	7	7
Measured prey items	**108**	**79**	**259**	**153**
Caterpillar	88	65	106	57
Other arthropod	13	10	40	66
Non-arthropod	1	1	59	10
Unidentified	6	3	54	20

First, we used this prey type categorization data to compare (1) the proportions of caterpillars, other arthropods and non-arthropod food items between broods (unidentified prey items excluded). Second, we calculated (2) the feeding rate for each brood as the number of feeding visits in 60 minutes (both parents combined; and including unidentified prey items and uncertain events) divided by the number of nestlings counted before the recording. Third, to determine the amount of nestling food, we calculated prey volume for each prey item from screenshots following the method described in ***Chapter III, IV***.

Due to the position of the camera (sideways), we were able to measure 375 prey items accurately. In those cases, when the prey items were visible but not measureable (e.g. the parent bird did not stand in front of the entrance hole) we used the extrapolation method introduced in ***Chapter IV***. Due to this process, we were able to estimate volume for an additional 224 prey items; resulting in prey size data for a total of 599 prey items, as shown in Table V.2 (uncertain events were excluded, but unidentified measured prey items were included). From these data regarding prey volume, we calculated (3) the average prey volume for each brood (i.e., the amount of food delivered per feeding event), as the average volume of the prey items whose volume we were able to estimate during the 60-min observation (Table V.1A). We also estimated (4) the volume of each individual caterpillar using the method described above (Table V.2; unidentified prey items and uncertain events excluded).

Finally, we used three variables to measure the differences in breeding success between first and second broods separately in forest and urban habitats (Table V.1B). (5) Maximum brood size was estimated as the maximum number of potentially hatched nestlings in a brood (calculated as the maximum number of eggs observed in the nest minus unhatched and broken eggs; Table A5.3). We also recorded (6) nestlings' body mass at ringing age (day 14–17 post-hatch), and (7) nestling survival as the number of ringed nestlings divided by the maximum brood size. For the analyses of reproductive success and nestling diet we used the same 32 pairs.

Statistical analyses

We conducted all statistical analyses in R 3.4.3. (R Core Team 2017) using the following packages: 'nlme' (Pinheiro et al. 2017), 'emmeans' (Lenth 2018), 'MASS' (Venables and Ripley 2002), 'car' (Fox and Weisberg 2011), and 'multcomp' (Hothorn et al 2008). In general, our data analysis consisted of two consecutive steps. In the first set of models (step 1), we compared the first and the second broods within study sites. In step 2, we ran additional post hoc analyses that combine information from the two urban and the two forest sites to respectively compare first and second broods within habitat types. For the latter purpose, we applied pre-planned pairwise comparisons and followed the approach suggested by Ruxton and Beauchamp (2008) as this method is a powerful approach to test a priori hypotheses. We used this two-step approach rather than including habitat type as a fixed effect and site as a random effect in the models because variance estimates of random effects with few levels (only four in our case) are unreliable (Bolker et al 2009, Vincze et al 2019). Furthermore, including both habitat type and site as fixed effects in the same model would lead to multicollinearity that would make our model estimates unreliable (Dormann et al 2013). Note that two variables (composition of the non-caterpillar fraction of the nestling food and nestling survival; Table V.1) were examined using Fisher's exact test and paired t-test, respectively, rather than mixed-effects models (see details in the respective sections below).

Within-site comparisons between first and second broods (step 1)

In the first step, for each specific response variable (see Table V.1), we fitted a statistical model (see below) that included study site (four sites) and brood type (first/second) as predictor variables, and also their two-way interaction. In addition, each model contained the following potentially confounding variables: in the models testing the amount and composition of nestling food we added year, date of observation, and time of the day; in the analyses of maximum brood size we added only year; in the model of nestlings' body mass we added year and nestling age (Table V.1). Year was included in the models as a three-level factor (2014, 2015, 2016). Because the onset of the first and second broods varied between sites and years, we mean-centered the date of observation separately for each site, year, and brood type (first, second) combination in order to express the relative dates of video recordings for each population. To do this, we determined the hatching date of the first nestling for each site and year combination, separately for the first and second broods, and all observation dates were calculated relative to these dates. This transformation reduced the multicollinearity of the date variable with year, site, and brood type in the models ($VIF_{max} < 1.8$ in all cases). The time of the day variable was categorized as a three-level factor: between 8–11 h ($n = 21$ records), 11–13 h ($n = 18$ records), 14–17:05 h ($n = 25$ records). Nestling age was a four-level factor (14, 15, 16, and 17 days old). We removed these additional confounding variables stepwise (by looking at the p-values in a type 3 ANOVA table generated from the initial and reduced models) until only statistically significant ($p < 0.05$) confounding variables and the main predictor variables (site, brood type, site × brood type) remained in the model. Because each pair has data from two broods in the analyses, we used pair ID as a random factor in all models. No pairs were included in these analyses from more than one breeding season. For each model, we checked the statistical assumptions of the models by examining the residual plots (Zuur et al 2009; see Appendices for the diagnostic figures for each final model, Figure A5.1.). We describe the details specific to each model below (because the predictor variables and model selection methods are common in each model, as described above, these are not repeated).

We examined seasonal differences in two aspects of food composition (i.e., prey types). First, to investigate the (1) proportion of caterpillars in nestling food (Table V.1A), we built a generalized linear mixed model (GLMM) with binomial error distribution and 'logit' link. Here, we used a binary response variable for prey type coded as caterpillars = 1, and all other identified food items = 0 (594 prey items; Table V.2). In this model, we added brood ID nested in pair ID as a random factor to control for repeated feeding events by the same pair. The difference between these two random factors is that the brood ID groups the feeding events belonging to one 60-minute observation, whereas pair ID connects the recordings of a pair's first and second broods. Second, we investigated the composition of the non-caterpillar fraction of the nestling food. However, since almost all non-caterpillar food items were classed as 'other arthropods' in the forest (we observed 'other' prey items only in two feeding events), we ran this analysis only in the urban habitat. Because the sample size was very low for some prey types even in the urban habitat (Table V.2), we used Fisher's exact test (instead of a linear model) to compare the ratio of non-caterpillar arthropod and non-arthropod food items between first and second urban broods (urban sites combined here). Only identified prey items were included in both food composition analyses (594 prey items in total; Table V.2).

Next, we conducted three analyses to investigate how the amount of nestling food varies between first and second broods (Table V.1A). We built separate linear mixed-effect model (LME) with the following response variables: (2) feeding rate, (3) average prey volume, and (4) caterpillar volume. In the models of feeding rate and average prey volume, we included pair ID as random factor, whereas in the caterpillar volume model we added brood ID nested in pair ID as random factor due to multiple data per brood. Caterpillar volume data were cube root transformed to meet the statistical assumptions of the models (Zuur et al 2009). Regarding feeding rate and average prey volume we ran the models allowing variance differences between the groups but it did not change qualitatively the results (Table A5.4.).

To investigate breeding success, we built separate linear mixed-effect models (LME) for (5) maximum brood size and (6) nestlings' body mass as response variables (Table V.1B). In the model of maximum brood size, we included pair ID as random factor, whereas in the nestlings' body mass model we added brood ID nested in pair ID as random factor. To analyse (7) nestling survival we used paired t-test, where we compared the average difference in nestling survival of first and second broods of each pair separately for forest and urban habitats (data of the sites within a habitat are combined here). Regarding nestlings' body mass we ran the models allowing variance differences between the groups but it did not change qualitatively the results (Table A5.4.).

Within-habitat comparisons between first and second broods (step 2)

In the second step of the analyses, we applied pre-planned pairwise comparisons to test the predictions separately for urban and forest habitats. To do this, we calculated marginal means of the response variables from the 'final' (after selection) models for first and second broods of each of our study sites using 'emmeans' package (Lenth 2018). Then, we calculated linear contrasts between first and second broods separately for urban and forest habitats (i.e., urban and forest study sites combined, respectively) from these marginal means derived from the models, and we used function 'glht' (in package 'multcomp') to test whether these contrasts (i.e., the difference between first and second broods) differed from zero within each habitat type. We applied the false discovery rate (FDR) method to correct p-values for multiple comparisons. In all analyses, we refer to $0.05 < p < 0.1$ as a marginally non-significant trend effect.

5.3. Results

Food composition

The statistical model for the (1) proportion of caterpillars in the nestling diet showed that the effect of the site × brood type interaction was not significant (Table V.3A). The within-habitat linear contrasts indicated that forest great tit nestlings received a similar proportion of caterpillars in the first and second broods (89.2 % vs. 84.3 %; Table V.3B, Figure V.1). However, in the urban habitat, nestlings reared in second broods tended to receive a smaller proportion of caterpillars than those in the first broods, although this difference was marginally non-significant (first vs. second broods: 55.9 vs. 43.4 %; Table V.3B, Figure V.1). We found a significant association between brood types and the types of the non-caterpillar fraction (i.e., non-caterpillar arthropods versus non-arthropods) of nestling diet in the urban habitat (Fisher's exact test, $p < 0.001$). Here, nestlings in second broods received higher proportions of other arthropods than other prey items compared to first broods (Figure V.1). Other (i.e., non-arthropod) prey items were negligible in the diet of forest broods (Figure V.1).

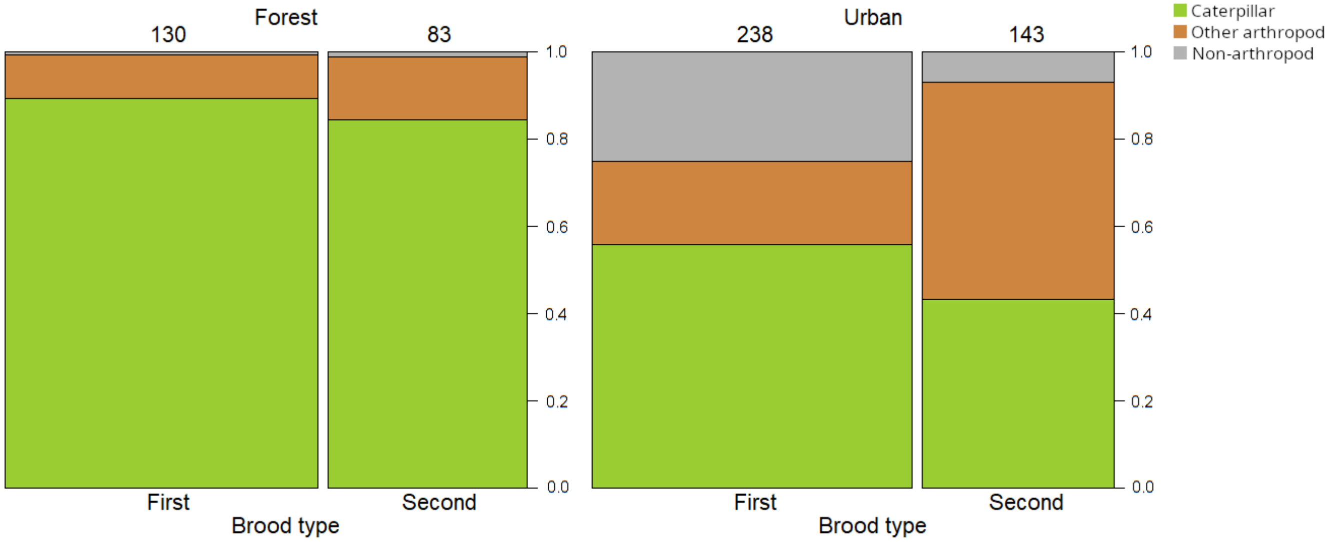


Figure V.1. *Proportions of prey types (caterpillar, other arthropod, and non-arthropod) that forest and urban great tit nestlings received in first and second broods. Sample sizes of identified prey items are shown above the columns and within a panel are proportional to the width of the columns.*

Table V.3. *Comparison of the composition and amount of nestling food between first and second broods in forest and urban habitats. Results of GLM/LM models (A) and the derived linear contrasts (B) (first broods compared to second broods in each habitat type) in the proportion of caterpillars in nestling food, feeding rate (number/nestling/hour), average prey volume (*mm^3*/feeding visit), and caterpillar volume (*mm^3*/specimen). Statistically significant (*$p < 0.05$*) differences are highlighted in bold, whereas marginally non-significant trend effects (*$0.05 < p < 0.1$*) are in italics. For linear contrasts, positive estimates indicate higher values in first broods. P-values were adjusted using the false discovery rate (FDR) method. Note that the rows are for different information in parts (A) and (B). Sample sizes (first vs. second broods): prey type (forest, 130 vs. 83; urban, 238 vs. 143 identified prey items); feeding rate, average prey volume (forest: 10 vs. 10 broods; urban: 22 vs. 22 broods); caterpillar volume (forest: 88 vs. 65; urban: 106 vs. 57 caterpillar specimens).*

(A) GLMM/LME models				**(B) Linear contrasts between first and second broods in forest and urban habitats**			
Predictors	**DF**	**χ2**	***p*-value**	**habitat**	**contrast ± SE**	**t**	**adjusted *p*-value**
Caterpillar vs. non-caterpillar (GLMM)							
Site	3	32.165	**< 0.001**	Forest	0.723 ± 0.694	-	0.306
Brood type	1	3.555	*0.059*	Urban	0.772 ± 0.335	-	*0.057*
Site × brood type	3	1.112	0.774				
Random effects:		**SD**					
Pair		0.000					
Brood nested in pair		0.505					
Residual variance		0.958					
Feeding rate (LME)							
Site	3	1.476	0.688	Forest	0.209 ± 0.474	0.441	0.663
Brood type	1	1.228	0.268	Urban	0.526 ± 0.305	1.724	0.191
Year	2	6.887	**0.032**				
Site × brood type	3	0.338	0.953				
Random effect:		**SD**					
Pair		0.516					
Residual variance		0.848					
Average prey volume (mm^3; LME)							
Site	3	1.765	0.623	Forest	-23.840 ± 67.100	-0.355	0.895
Brood type	1	0.184	0.668	Urban	6.059 ± 45.418	0.133	0.895
Year	2	9.491	**0.009**				
Site × brood type	3	0.425	0.935				
Random effect:		**SD**					
Pair		0.012					
Residual variance		120.032					
Caterpillar volume (mm^3; LME)							
Site	3	6.204	0.102	Forest	-0.153 ± 0.527	-0.290	0.775
Brood type	1	0.462	0.497	Urban	-0.605 ± 0.431	-1.404	0.347
Site × brood type	3	1.961	0.581				
Random effects:		**SD**					
Pair		0.000					
Brood nested in pair		0.697					
Residual variance		1.533					

Amount of nestling food

Regarding (2) feeding rate, we found that site × brood type interaction was not significant (Table V.3A). Linear contrasts calculated from this model did not indicate any significant difference in the feeding rate between first and second broods either in the forest or in the urban habitats (Table V.3B, Figure V.2A). Similarly, comparison of the (3) average prey volume, the site × brood type interaction was not significant (Table V.3A), and linear contrasts between first and second broods also showed no significant differences either in the forest or in the urban habitats (Table V.3B). This observation indicates that in both habitats the size of the prey items per feeding visit was similar between first and second broods (Table V.3B, Figure V.2B). For (4) caterpillar volume, we also found that site × brood type interaction was not significant (Table V.3A) and linear contrast showed that the volume of caterpillars did not differ between first and second broods either in the forest or in the urban habitats (Table V.3B, Figure V.2C). Year had a statistically significant effect on the feeding rate and average prey volume models, but not on the caterpillar volume model.

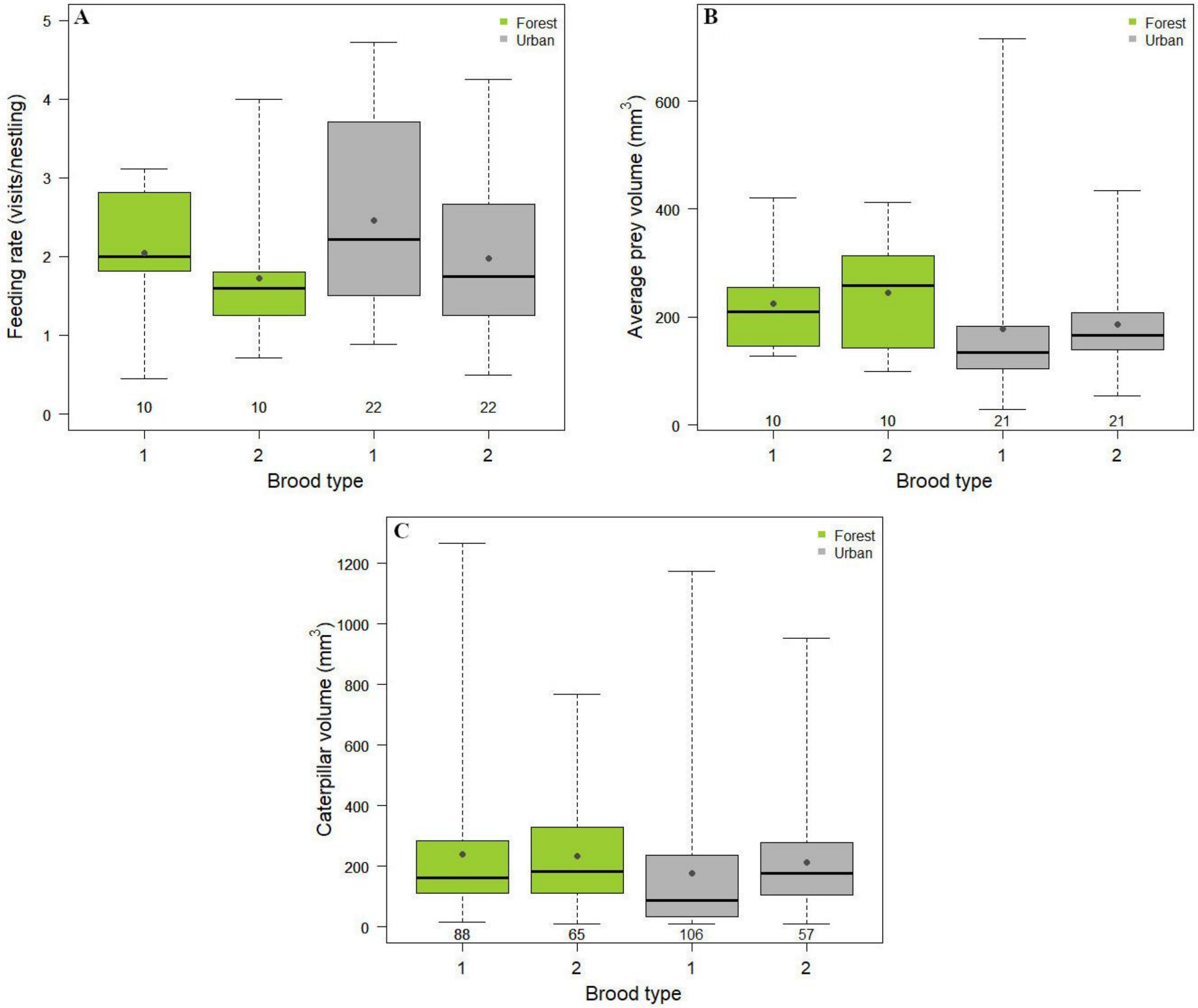


Figure V.2. *The amount of food delivered to great tit nestlings during 60-min video observations in first and second broods in forest and urban habitats: A, feeding rate of parents (number/nestling/hour); B, average prey volume delivered by the parents to nestlings (mm3/feeding visit); C, the volume of caterpillar specimens delivered to great tit nestlings (mm3). Boxplots show the median (thick lines), mean (dark dots) and the interquartile range, with the whiskers representing the range of data distribution. Sample sizes (number of broods for feeding rate and average prey volume, number of specimens for caterpillar volume) for each group are provided below the boxes.*

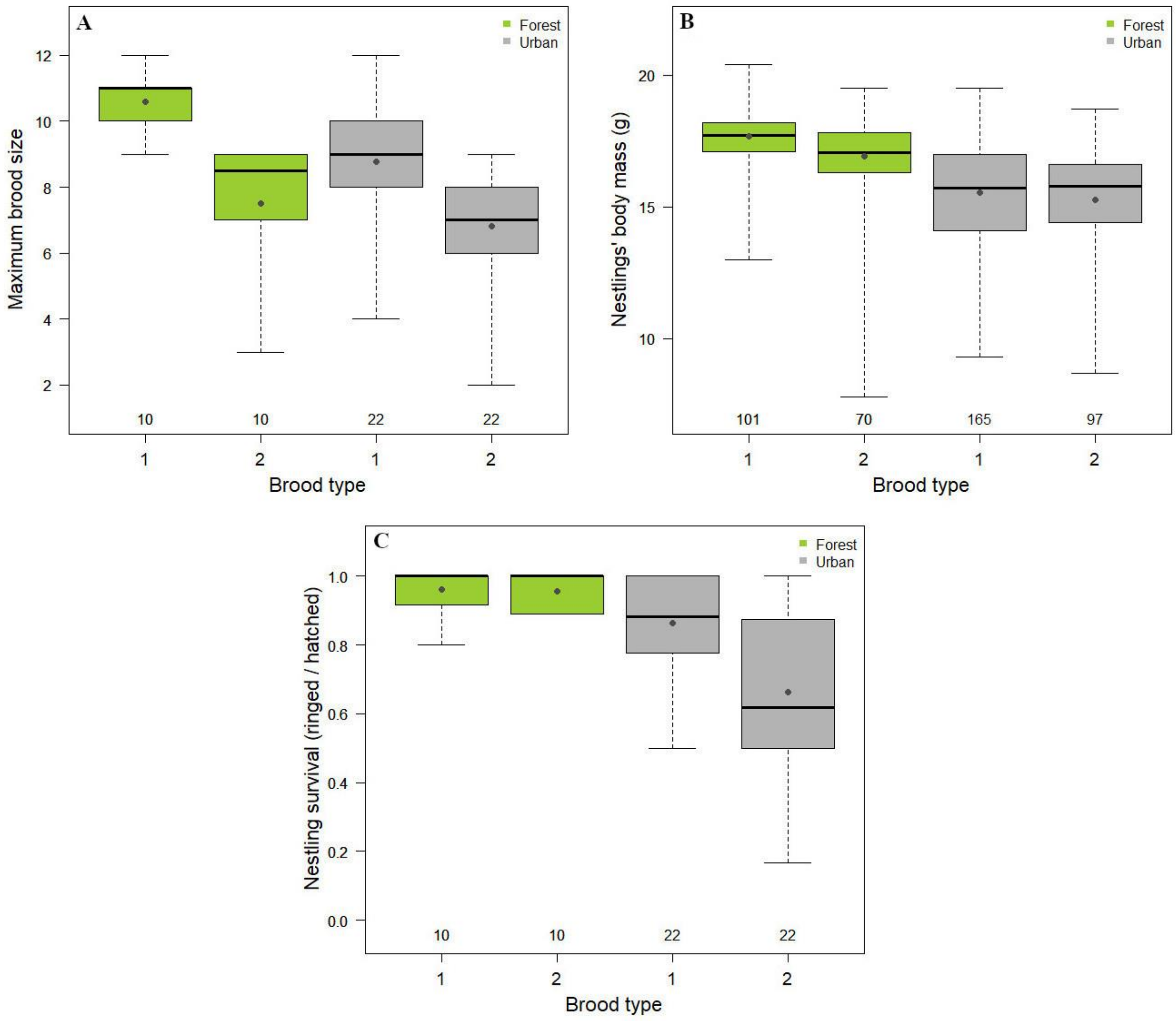
Breeding success

For (5) maximum brood size, we found that site × brood type interaction was not significant (Table V.4A). Linear contrasts calculated from this model indicated that both in urban and forest habitat, maximum brood size decreased seasonally, meaning that parents in second broods reared fewer nestlings than in first broods regardless of habitat type (Table V.4B, Figure V.3A). When comparing (6) nestlings' body mass, we also found that site × brood type interaction was not significant (Table V.4A). Linear contrasts between first and second broods showed no significant differences either in the forest or in the urban habitats, meaning that nestlings' body mass at ringing age did not differ between first and second broods (Table V.4B, Figure V.3B). (7) In the urban habitat we observed a significant difference in nestling survival between first and second broods (average difference in nestling survival rate between first vs. second broods: 0.201; $t = 4.157$; $df = 21$; $p < 0.001$, $n=22$ broods; Figure V.3C). In contrast, we did not detect significant differences between first and second broods in the proportion of nestlings that survived from hatching to ringing in the forest habitat (average difference in nestling survival between first vs. second broods: 0.007; $t = 0.23$; $df = 9$; $p = 0.823$, $n = 10$ broods; Figure V.3C). The year had a statistically significant effect on the nestlings' body mass but not on maximum brood size.

Table V.4. *Comparison of breeding success between first and second broods in forest and urban habitats. Results of LME models (A) and the derived linear contrasts (B) (first broods compared to second broods for each habitat type) in maximum brood size and nestlings' body mass (g). Statistically significant ($p < 0.05$) differences are highlighted in bold, whereas marginally non-significant trend effects ($0.05 < p < 0.1$) are in italics. For linear contrasts, positive estimates indicate higher values in first broods. P-values were adjusted using the false discovery rate (FDR) method. Note that the rows are for different information in parts (A) and (B). Sample sizes (first vs. second broods): maximum brood size (forest: 10 vs. 10 broods; urban: 22 vs. 22 broods); nestlings' body mass (forest: 101 vs. 70; urban: 165 vs. 97 nestlings).*

(A) LME models				**(B) Linear contrasts between first and second broods in forest and urban habitats**			
Predictors	**DF**	**χ2**	***p*-value**	**habitat**	**contrast ± SE**	**t**	**adjusted *p*-value**
Maximum brood size							
Site	3	7.6406	0.054	Forest	2.88 ± 0.719	4	**< 0.001**
Brood type	1	7.32	**0.007**	Urban	2.04 ± 0.463	4.413	**< 0.001**
Site × brood type	3	3.119	0.374				
Random effect:		**SD**					
Pair		1.233					
Residual variance		1.286					
Nestlings' body mass (g)							
Site	3	16.218	**0.001**	Forest	1.053 ± 0.659	1.599	0.242
Brood type	1	1.373	0.241	Urban	-0.157 ± 0.447	-0.352	0.728
Year	2	9.444	**0.009**				
Site × brood type	3	4.236	0.237				
Random effects:		**SD**					
Pair		0.357					
Brood nested in pair		1.084					
Residual variance		1.388					

Figure V.3. *Breeding success of the 32 video-recorded great tit pairs in first and second broods in forest and urban habitats: A, maximum brood size (number of potentially hatched nestlings); B, nestlings' body mass (in g); C, nestling survival (number of ringed nestlings / maximum brood size). Boxplots show the median (thick lines), mean (dark dots) and the interquartile range, with the whiskers representing the range of data distribution. Sample sizes (number of broods for maximum brood size and nestling survival, number of nestlings for nestlings' body mass) for each group are provided below the boxes.*



5.4. Discussion

In this study we explored the differences in nestling diet and reproductive success between first and second broods of the same breeding pairs in two habitat types that differed regarding the availability of caterpillars (the main component of nestling diet) during the breeding season. This design allowed us to study the potential effects of seasonal changes in food availability on reproductive success without the confounding effects of seasonally changing parental quality caused by the delayed breeding of low-quality pairs. Studies of second broods often examine the effects of a treatment on parental behaviour, observations without manipulation are relatively rare. Additionally, to the best of our knowledge, our study is the first to compare both the composition and the quantity of nestling diet between first and second broods in urban environments.

Regarding the (1) composition of nestling food, we found that in forest habitats nestlings both in first and second broods received high proportions of caterpillars (> 80%) and their diet did not differ significantly between the two brood types. In contrast, urban nestlings in second broods tended to receive lower proportions of caterpillars and higher proportions of other arthropod food items (e.g., spiders) than first broods. However, the amount of nestling food [(2) feeding rate, (3) average prey volume, (4) caterpillar volume] did not differ between first and second broods in either habitat. Regarding breeding success, parents in both habitat types reared (5) fewer nestlings in second broods. However, nestlings' (6) body mass did not differ between first and second broods. In the forest habitat, almost every hatched (7) nestling survived in both first and second broods. In contrast, urban nestlings in second broods had cc. 20% lower survival than first broods. We discuss these results in detail separately for each habitat type. Please note, however, that due to the low number of sampled pairs (especially in the forest habitat) some of the results should be treated with caution.

In forests, neither the composition nor the amount of food per nestling differed significantly between first and second broods. These results imply that even though caterpillar biomass decreased as the season progressed (Seress et al 2018), great tit parents were able to deliver an approximately similar composition and amount of food to their nestlings. This may be feasible due to the lower brood size in second broods, a strategy that may be a response to the reduced food availability later in the season. As a result of fewer nestlings yet similar nestling diet, forest nestlings reached a high body mass and survival similar to that high in first broods. Although the relationship between the phenology of caterpillar abundance and breeding success has been observed in long-term studies including a forest tit species - the green-backed tit *Parus monticolus* (Shiao et al 2019) - , complex analyses of nestling diet (both the composition and amount) are rare, thus making comparison of results between studies difficult. Studies that examine the temporal changes of feeding rate without prey size, for example, may have inconsistent results because parental provisioning activity can vary with prey size (Senécal et al 2021). Furthermore, some studies found a seasonal decline in feeding rate (Schwagmeyer and Mock 2003, Barba et al 2009) while others found no seasonal patterns (Bortolotti et al 2011). Regarding food composition, in an orange grove, Barba et al (1990, 2004) found that the proportion of caterpillars in the nestling diet of great tits decreased over the season and adult moths became the most frequently provided food for the nestlings. The authors considered that the short period of caterpillar peak forced the birds to change and adapt prey type to seasonal availability and abundance. Another study from an evergreen forest in Corsica also observed that the proportion of caterpillars in blue tit nestlings' diet decreased later in the season, again suggesting a marked limitation of this prey in the area as the season progressed (Bańbura et al 1994). However, Lambrechts et al (2008) found different patterns in different types of forests. They reported a seasonal decrease in frass fall (a proxy of caterpillar biomass), clutch size, and the number of fledged young in a downy oak *(Quercus humilis)* forest patch, and a seasonal increase of these characteristics in a holm oak *(Quercus ilex)* forest patch. Conversely, it seems that great tits in the forest population in our study were able to find enough caterpillars for their nestlings even later in the season to successfully rear the late-born nestlings mostly on that prey type, without needing to switch to other less optimal food types. Note, however, that beside caterpillars, other arthropods may also be important components of the nestling diet (e.g., spiders, Pagani Núñez et al 2011).

In the urban habitat, we found that parents tended to provide fewer caterpillars to nestlings in second broods, and also that nestling survival was lower in second broods than in first broods. Although urban areas showed smaller caterpillar peaks and less pronounced caterpillar biomass decline throughout the breeding seasons of 2013-2016 (i.e., a period overlapping with that of the current study; see Figure 2 in Seress et al 2018) in our study the proportion of caterpillars in nestling diet decreased for second broods. Similarly, to the forest pairs, urban great tits also reduced their brood size in second broods, possibly as a response to declining food availability, and therefore, they were able to deliver similar amounts of food to their nestlings. In parallel with this, we found decreased nestling survival in first vs. second urban broods, possibly due to the lack of optimal food items, i.e., caterpillars. However, the surviving nestlings reached similar body mass in first and second seasonal broods. The combination of these results suggests that the adjustment of brood size to the local food supply is not optimal in our urban sites as, despite the smaller brood sizes, nestling survival was still lower in second broods. Although complex investigation of seasonal changes of nestling diet in urban habitats is rare, a study in Poland examined great tit nestlings' haemoglobin concentration in first and second broods in a parkland area that was characterized by highly fragmented tree cover and intense human disturbance (Kaliński et al 2009). The authors found food shortages for second broods in a year characterized by dry and hot weather (which was not optimal for arthropod development). This resulted in lower haemoglobin levels but similar body mass of the nestlings compared to first broods. In contrast, in another year, the milder weather (moderately warm temperature with regular but not heavy rain) enabled the development of rich arthropod communities, and the haemoglobin concentrations in the blood of second brood nestlings were even higher and the birds were in a better condition than those in first broods. In a Portuguese suburban forest, Norte et al (2008) also found that nestlings from second broods had significantly lower haemoglobin levels and a tendency to a lower body condition index. They also hypothesized that these results could reflect malnutrition of the nestlings.

Our results, in summary, imply that our urban habitat might be similar to the above-mentioned 'poor' quality forest habitat, where great tits are forced to switch from the preferred, optimal caterpillar prey items to other, less nutritious food types. A possible explanation for the difference we found in nestling food composition between first and second urban broods could be a difference in territory quality (i.e., second broods being in lower quality territories; Bańbura et al 1994). Indeed, in our study, 15 of the 22 urban great tit pairs (68.2 %) moved to a different nest box for their second brood. However, they mostly chose neighbouring nest boxes (distance between the occupied nest boxes in first and second broods, mean ± SE: 43.6 ± 4.4 m). A recent study from Scotland found that chick-rearing blue tits in an urban parkland area flew c. 40 m for food on average (Jarrett et al 2020), and our own data also indicate that urban great tits mostly use a 60-m radius area around a nest (Seress et al *in prep.*). Territories are thus probably overlapping considerably for first and second broods of the same urban pairs. Interestingly, in the forest, only 2 of the 10 forest parents (20 %) changed nesting site for second broods in the same breeding season (distance between the two occupied nest boxes was 91 and 30 m for the two pairs, respectively), while the rest of eight parents stayed in the same nest box (and territory) for both broods. It is therefore unlikely that differences in territory quality between first and second broods could have affected our results.

It is important to note that there may be other effects in the background that we did not assess in this study but that could also reduce nestling survival in the urban habitat. For example, our earlier study showed that the number of hot days can increase nestling mortality (Pipoly et al 2022) and as the season progresses, the frequency of hot days are likely to increase. However, in our study system, we found that the negative effects of hot weather on urban nestlings' body mass and survival were minor or less harmful to nestlings than in forests (Pipoly et al 2022). On the other hand, ectoparasites can also influence parental provisioning (Schoepf et al 2022) or reduce nestling body conditions (O'Brien and Dawson 2008), and high levels of parasite load can lead to nestling mortality. For example, an experimental study on house martins *(Delichon urbica)* in Badajoz city, Spain, showed that the ectoparasitic house martin bug *(Oeciacus hirundinis)* had higher negative effects on its host's reproduction during second clutches than in first clutches when environmental conditions for reproduction were deteriorated (de Lope et al 1993).

As we highlighted in the Introduction, the parental quality and date hypotheses are most likely non-mutually exclusive, and manipulation of breeding time without unwanted side effects seems to be impossible (reviewed in Verhulst and Nilsson 2008). Although our study does not allow for a clear separation of the two hypotheses, it does not seem that the reduced nestling survival for urban second broods is a consequence of parental feeding capacity (parental quality hypothesis), but is caused rather by the decrease of optimal food in nestling diet (date hypothesis). In our study, we aimed to control for parental quality by quantifying the feeding activity and breeding characteristics of the same parents within a breeding season. This observation method could also have disadvantages however. For example, parental quality may not be constant over time. Some studies have reported weight loss in females during the breeding season and this, may affect parental care (De Laet and Dhondt 1989). Interestingly, we did not detect differences in feeding rate, suggesting that summarized parental care (female and male combined) per nestling was stable in both habitats during the breeding season. Also, reduced brood size for second broods seems to be a successful strategy of parents to maximize reproductive output when optimal nestling food is limited/declined. Parents' age can also impact parental success (Perrins and McCleery 2008). Older birds for example might be more experienced in searching for high quality food than first-year breeders. In our study, the proportion of young parents (< 2 years old) relative to the older parents in the two habitat types was similar (0.25 in both habitats, Table A5.2). This also supports the theory that, rather than parental experience, a limited food supply is the key factor regulating breeding success of great tits in our urban habitat.

Last but not least, our previous findings showed that our urban habitat is strongly food limited during first broods (Seress et al 2018, 2020; Sinkovics et al 2021). Our results from the present study strengthen and expand this earlier conclusion in that the shortage of optimal nestling food (caterpillars) in the cities is even more pronounced as the season progresses, presumably driving the reduced survival of urban nestlings we observed in second broods. Although urban great tit pairs try to compensate for the lack of caterpillars by reducing brood size and switching prey type, they likely cannot fully avoid the adverse effects of reduced food quality. Thus, as in our earlier studies, we suggest that improving urban habitat quality by supporting arthropod communities (for example by planting native trees, using fewer pesticides in parkland and garden management, reducing mowing intensity, and creating new habitats by sowing wildflowers; Süle et al 2023) would likely enhance the breeding success of urban insectivorous birds. We would thus like to encourage city managers to take these findings and suggestions into account when planning future urban parks.

CHAPTER VI

General discussion

In my thesis I explored habitat and seasonal differences in the diet of great tit nestlings. In this final chapter, I summarize the main findings and conclusions, and also suggest some directions for future urban planning that supports wildlife and human well-being simultaneously.

In ***Chapter III***, we validated a commonly used method for quantifying nestling food from video recordings. Although using screenshots to determine prey size is a widespread method, its accuracy and repeatability have not been tested before. We found high accuracy and repeatability between the measurements, allowing researchers to characterize the provisioning efforts of bird species that deliver one food item per feeding visits (e.g. great tits). Additionally, given our high among-observer repeatability, measurements can be made by multiple observers if they are provided with a detailed description of the measurement protocol. However, it clearly turned out that the unfavourable position of the camera (sideways to the nest box) and the fast speed of some individual birds did not allow us to determine the exact size of all prey items. We also provided some solutions to reduce this difficulty. We concluded that for those studies where artificial nest boxes are applied, we recommend placing infrared-camera inside nest boxes for the purpose of examining nestling diet (e.g. O’Connor et al. 2010, 2014, Pagani-Núñez and Senar 2014, Navalpotro et al. 2016). This may make identification and measurement of prey items more effective because the camera can be placed in a more favourable position and adults generally move more slowly once they enter a nest box, making it easier to catch a clearly visible screenshot. However, there are hundreds of bird species that do not breed in artificial nest boxes (e.g. open-cup nesters), thus, placing cameras outside the nest is unavoidable. For these studies, the method for extrapolating prey size from partial measurements that we developed in this chapter could be a useful way to increase the number of measured samples.

The main aim of my doctoral field research (***Chapter IV, V***) was to investigate the effects of habitat and season on the diet of great tit nestlings. We have previously found that caterpillar biomass and reproductive success of great tits are strongly decreased in urban versus forest habitats during first broods except for a specific year (2014), and we also observed seasonal decline in caterpillar biomass in both habitat types (especially in the forests; see ***section 1.3. in Chapter I***). In my doctoral field studies, we extended this line of research and our main purpose was to find out whether the reason for the reduced reproductive success observed both between habitats and seasonally within habitats can be related to the nestlings' altered diet. In both cases, we found strong evidence for the food limitation hypothesis in our study system *(**Chapter IV, V**).*

In ***Chapter IV*** we investigated the habitat differences in nestling diet. We compared the composition and amount of nestling food between urban and forest habitats during the period of the first broods. We found that great tit nestlings in urban broods received decreased proportions of caterpillars but increased proportions of non-arthropod food items (e.g. seeds) compared to forests. Besides, urban parents were able to compensate for the smaller prey items by increasing their feeding activity, which ultimately resulted in urban nestlings receiving similar amount of food *per capita* as forest nestlings. We concluded that although urban great tit parents could provide the same quantity of food per nestling as forest parents by reducing their brood size and increasing the *per capita* feeding rates for nestlings, they could not fully compensate for the scarcity of high-quality prey items (caterpillars) as they experienced higher ratio of starvation-related mortality and their nestlings weighed lower. We also reported a specific year (2014) when the differences both in caterpillar biomass and in breeding success were the smallest between urban and forest habitats. In this year we found the smallest — and mostly non-significant — habitat differences in nestling diet. The annual changes in caterpillar size may provide a likely explanation for this result. In 2014 urban pairs delivered much larger (2.2 times larger on average) caterpillars compared to the other two years, similar in size to the caterpillars provisioned in the forest. Consequently, in this year urban parents were probably able to provide enough high-quality food for their nestlings, which resulted in improved nestling development. These results also highlight the important role of large-sized caterpillars in nestling diet, which hypothesis was also supported by other authors (Schwagmeyer and Mock 2008; Seress et al. 2012). However, why large prey items are so nutritious is still unclear. It is possible that the chemical composition of large caterpillars is different or that their nutrient content per unit mass is more favourable. In summary, this chapter highlighted that the decrease in the amount of caterpillars in the environment (i.e. in tree canopies) caused by urbanization is reflected in the food composition of the nestlings, and this is a likely cause of the commonly observed higher mortality and reduced weight gain of urban nestlings. Importantly, the food limitation hypothesis was also experimentally supported in our study system when some urban nests were provided with extra mealworms during the chick-rearing period (Seress et al. 2020). This additional good quality food provided to urban nestlings resulted in substantially larger body size and higher survival rates that were similar to their unsupplemented conspecifics in a forest habitat (Seress et al. 2020).

In ***Chapter V***, we examined the seasonal changes in nestling diet and breeding success separately within urban and forest habitat. We selected great tit pairs that had both first and second broods within the same breeding season and made video observations on the parents' feeding activity to determine the composition and amount of nestling food. In forests, neither the composition nor the amount of food per nestling differed significantly between first and second broods. These results imply that even though caterpillar biomass decreases as the season progresses (Seress et al. 2018), great tit parents in forests are able to deliver approximately similar composition and amount of food to their nestlings. This may be feasible due to the lower brood size in second broods, which strategy is probably a response to the limited food availability later in the season. As a result of these two characteristics of breeding and diet in second broods (fewer nestlings and similar quality of nestling diet), forest nestlings reached similarly high body mass and survival as they did in the first broods. In contrast, although urban birds could also provide similar amounts of food to their nestlings in the first vs. second broods, their second brood nestlings' diet tended to contain fewer caterpillars. In parallel with this, we detected decreased nestling survival in urban second broods, possibly due to the lack of optimal food items, i.e. caterpillars. However, the surviving second brood nestlings could reach similar body mass compared to first broods. Overall, similarly to the forest pairs, urban great tits also reduced their brood size late in the season, possibly as a response to the seasonal decline of caterpillar biomass. However, the combination of these results suggests that the adjustment of brood size to the decreased local food supply alone is not enough in our urban sites, because mortality during the nestling stage remained frequent in these broods.

Both field studies ***(Chapter IV, V)*** revealed that the lack of high-quality food cannot be fully substituted with higher quantity of other food types. This was experimentally proven on adult house sparrows which were fed with bar snacks in captivity, which are one of the most ubiquitous food sources for them in urban habitats. However, bar leftovers are high in carbohydrates and fat but low in protein, and their nutritional content is significantly divergent compared to their natural food. The modified diet was reflected in the poorer physical condition of the birds, e.g. they had depleted energy reserves and showed the symptoms of malnutrition (Bernat-Ponce et al. 2023). However, interestingly, despite the overwhelming evidence that urban and non-urban habitats differ in caterpillar availability and that urban insectivorous birds suffer inferior breeding success compared to natural habitats, nestling diet does not always differ in urban compared to natural areas. For example, Grabarczyk et al. (2022) found that urbanization had clear impacts on the survival and condition of house wren nestlings (urban broods contained fewer, smaller nestlings), but their diet composition were similar. One potential explanation for this finding might be the difference in nutrient content of prey types. Some earlier studies found that urban plants and caterpillars often have lower carotenoid content compared to natural habitats (Isaksson and Andersson 2007; Isaksson 2009) which is probably due to the impact of environmental stress on urban trees (Isaksson 2009). This difference in nutrient content can further reduce the nutrient supply of urban nestlings. Consequently, even if urban nestlings grow up on the same types of diet as their forest counterparts, they may still suffer from some nutrient deficit.

Contrary to our results, some studies revealed that urbanization does not necessarily result in significantly lower breeding success and altered diet in small passerine species (Stracey and Robinson 2012; Marini et al. 2017; Hajdasz et al. 2019). One plausible explanation is the variance in the degree of urbanization among studies. The influence of urbanization on breeding success and nestling diet may depend on the environmental characteristics of a given city and, particularly, on the characteristics of the occupied territories. For example, a 7-year-long study revealed that urban tits were less likely to breed in territories dominated by non-native trees and great tit nestlings weighed significantly less in these territories compared to those with fewer non-native trees (Jensen et al. 2023). Similar results were found by Narango et al., namely that native compared to non-native plants were more likely to host higher biomasses of caterpillars and that Carolina chickadees *(Poecile carolinensis)* strongly preferred to forage on native than on non-native plants during breeding (Narango et al. 2017, 2018). As a consequence, urban matrix is rather heterogeneous when it comes to vegetation composition, there is a large variance in territory quality from the birds’ perspective. Furthermore, the ecological conditions of the studied cities can highly vary due to various geographical, climatic, and economic reasons. Last but not least, the contradictory results may also suggest that although insufficient natural food supply during the breeding season may be one key factor regulating urban population sizes of insectivorous birds, it is not the only one. This idea is supported by some other food supplementation experiments (i. e. when additonal, high quality food is provided to nestlings) that had various effect on urban birds. Some of these have found only a small positive (Meyrier et al. 2017) or even negative (Charmantier et al. 2017) impacts on body size and/or nestling survival.

Overall, as pointed out in ***Chapter I***, the impact of urban environments may arise from the intricate interactions among several environmental factors including different forms of pollution, altered species community and abundance, intense human presence, predation pressure, and so forth. However, the effects of environmental variables are usually examined separately (e.g. the impact of light pollution), and for further research it would be worthwhile to consider their additive effects and interactions as well. Furthermore, the results of the two field studies also highlight that long-term studies on urban populations with robust sample sizes are needed to fully understand the implications of among-year variation in environmental conditions.

Suggestions for urban planning

The results of my PhD study support the growing body of evidence suggesting that urban habitats might be strongly food limited during the whole breeding period for some insectivorous birds. As a consequence, increasing the abundance and diversity of phytophagous insects in cities would likely enhance not only the breeding success of urban insectivorous birds (Planillo et al. 2021), but also other insectivorous groups, which are also affected by the negative effects of urbanization (Callaghan et al. 2021; Theodorou 2023). To the general public, helping urban phytophagous insects, often perceived as pests, may seem counterintuitive, but they are ecologically important species that enhance biodiversity by providing diet for insectivorous animals, as well as being pollinators in their adult life stage.

We can help urban arthropods in several ways. First, collecting and removing the vegetation in autumn from parks and urban gardens (grass, fallen leaves, branches) is a general, non-wildlife-friendly habit of urban management. Understory plant litter provides food for decomposers, shelters and a place to hibernate, oviposit and forage for many arthropod species, and also increases habitat heterogeneity (Peng et al. 2020). Thus, composting and/or leaving the understory plant litter on the ground at some places would be not only beneficial for urban arthropod diversity but would also save money. Second, a recent study on declining European butterfly populations suggested that simple measures such as reducing mowing intensity or creating new habitats by sowing wildflowers could also produce quick wins (Warren et al. 2021). Similar results were found by another study which investigated the impact of rare mowing and annual flower-sowing treatments on pollinators, floral resources, and vegetation characteristics in urban locations including the city of Veszprém where our studies were conducted. The field experiment found that the less frequently mown public areas had higher and greener vegetation with more flowers and pollinators (Süle et al. 2023). Authors of this latter paper concluded that in order to create and maintain diverse urban ecosystems the best choice would be to combine two types of treatment, namely overseeding the green areas with native and mostly perennial seeds and maintaining them with a mosaic mowing system (Süle et al. 2023). Third, planting native trees at higher densities could also increase caterpillar populations at the canopy level and, indirectly, the reproductive success of insectivorous birds (Burghardt et al. 2010; Mackenzie et al. 2014; Tallamy and Shriver 2021). Remeš tested this hypothesis and compared the breeding density and success of blackcaps *(Sylvia atricapilla)* in territories covered by introduced vegetation to those covered by native plants. He found that although blackcaps preferred to nest in the non-native vegetation, they experienced lower breeding success there. This combination of results suggests that human-modified habitats can function as ecological traps by luring settling birds into unsuitable habitats (non-native plants), possibly leading to demographically non-self-sustaining populations (Remeŝ 2003). Furthermore, exotic plant species also tend to support less diverse arthropod fauna than native species due to several reasons. For example, exotic plants may produce novel secondary compounds that are toxic to native herbivores, induce behavioural changes in arthropods, and even change the performance of insects (reviewed in Bezemer et al. 2014). Supporting this, a study from North America found that native plants produced five times more total arthropod biomass and up to seven times more arthropod species compared to non-native plants (Ballard et al. 2013). Furthermore, to avoid the emergence of undesired plants, urban park gardeners and property owners often use herbicides, which are proven to have various harmful effects on wildlife including physiological and behavioural changes in individuals (Sharma et al. 2020; Talyn et al. 2023; highlighted in ***Chapter I***). Thus, the forth way to enhance the diversity and biomass of urban arthropod fauna is to reduce the use of such chemicals. Additionally, it must be noted here that creating pesticide-free urban green parks might also reduce health risks to humans. Despite marketing efforts by the chemical industry, a growing amount of evidence demonstrates that human exposure to chemical pesticides and herbicides is linked to serious disorders such as various cancer types, heart, respiratory and neurological diseases, increased vulnerability to Parkinson’s disease, reduced cognitive functions and so forth (reviewed in Islam et al. 2022). Since pesticides remain in the environment for decades and accumulate in animal and human tissues, the harmful effects of these chemicals on human health is probably still underestimated. For example, DDT, an insecticide, was banned across Europe in the 1980s but is still found in soil, water, living organisms (Mansouri et al. 2017) and also in human food such as dairy products (Năstăsescu et al. 2020). However, it is challenging to find up-to-date information on the type and quantity of pesticides spread globally in the cities. Regarding New York City, the latest report states that in 2021 ‘pesticides were applied a total of 709,855 times by New York City agencies’, which included ‘7,327 gallons of liquid and 178,838 pounds of solid pesticide products’(~27 100 liter and 80 400 kg; New York City, 2021). Considering the above numbers and the fact that the spreading of chemicals does not stop at the boundaries of the treated areas, it should be considered that every day countless adults and children might be contact with these harmful chemicals in urban areas via respiration or absorption throughout the skin and there is no serious discussion about its potential risks (Md Meftaul et al. 2020). For example, a review found associations between even low-level pesticide exposure in children and the development of two neurocognitive disorders, ASD (autism spectrum disorder) and ADHD (attention deficit disorder with or without hyperactivity; Roberts et al. 2019). The risk is particularly high in developing countries where there are no strict legal regulations for the application of these chemicals (e.g. there are still many countries where DDT is not banned despite its proven harmful effect on human health). Consequently, in order to protect both human and ecosystem health, it must be considered to apply alternative, pesticide-free, eco-friendly urban park management practices globally.

The fifth way we can contribute to the conservation of urban (arthropod and overall) biodiversity and help the preservation of urban ecosystems is that we should reconsider the size and shape of urban green areas as well as create green corridors between them. As introduced in ***Chapter I,*** a growing number of evidence suggests that habitat fragmentation creates relatively more habitat edges, and the size and shape of individual patches can determine species' richness, diversity, abundance and genetic diversity. Compared to small spaces, larger green areas can encompass a wider range of microhabitats, niches, have more habitat heterogeneity including different soil types, resources, moisture levels, and vegetation types, which features all support overall biodiversity and reduce genetic loss (Soga et al. 2013). A study that examined the connection between ant, beetle and spider diversity and the features of nearly 50 parks in Taiwan found that larger parks had higher arthropod diversity (Peng et al. 2020). However, there is no general rule on the size of area required to maintain the high biodiversity in urban parks. According to Beninde et al. (2015) who conducted a meta-analysis based on data from 75 cities worldwide, to determine the threshold of the necessary area needed, the first task is to clarify the conservation objective. If the aim is to minimise the loss of urban adapter species, smaller patches might be adequate. However, larger areas are required if the plan is to protect also threatened or urban-avoider species. Furthermore, the shape of the green areas cannot be neglected due to the emergence of edge effect. Concave patches with complex shapes, such as irregular or jagged edges, tend to have a higher proportion of edge habitat relative to core habitat compared to patches with simpler, convex shapes. It should be noted here that below a certain patch size edge effect cannot be detected because all the centre areas of small patches are completely exposed to edge effects (Soga et al. 2013). Overall, in urban environment where small forest remnants dominate, simplifying the shape of the patches to maximise the core areas relative to the edges may be the most constructive means to preserve biodiversity (Soga et al. 2013). The formerly mentioned study from Beninde et al. (2015) also highlighted that a network of corridors between the green areas is at least as important from the point of view of urban biodiversity conservation as the size of the areas, since stepping-stone habitats limit the dispersal of many species. A case study supported this hypothesis which was researching the effect of urban green corridors on the diversity of spider, carabid and staphylinid taxa and found that corridors enhanced the dispersal of many of these species (Vergnes et al. 2012). Green corridors can also facilitate the genetic diversity of arthropod species such as bees, which were formerly reported to have high levels of inbreeding due to isolated populations (Chau et al. 2023). Nevertheless, the creation of such urban green corridors is a challenge because there are many property owners and stakeholders who need to be involved in this process (Zellmer and Goto 2022).

It is worth mentioning that a handful of recent studies in Europe suggest that planting food trees (e.g. nut and fruit trees) in community gardens can improve recreational and regulating services (e.g. carbon storage), and/or provides edible crops (Park et al. 2019). Food forestry is defined as "the skill and art of growing food in a way that replicates nature", for example, by creating "the multiple vertical layers" of perennial and annual plants that interact with each other and imitate the ecological processes of a natural forest (Park et al. 2018, 2019). Urban food forestry may serve as an innovative restoration model which holds numerous potential advantages, such as helping the restoration of forest functions and improving biodiversity. However, there are some challenges to consider (reviewed in Feldmann and Vogler 2021), as producing food in urban environment raises some important questions, for example, whether food grown in a polluted environment can be consumed at all, because the harmful chemicals probably accumulate in the plants' tissues.

A larger and more diverse urban ecosystem is not only beneficial for wildlife, but also benefits the human residents of cities. Human-nature relations have undergone significant changes in the past decades, which are more conspicuous in urban landscapes where people are surrounded by extremely high density of buildings, roads and impermeable surfaces which are not found in nature. Although urbanization has brought numerous benefits for the residents, such as improved access to healthcare, education, recreational and economic opportunities, the number of potential stress-inducing factors is also increased in cities. Numerous studies have examined the relationship between disconnection from nature and health problems (called 'nature-deficit disorder' by Richard Louv, 2005). For example, a study by White et al. (2019) found that spending just 2 hours per week in nature was associated with a significant increase in good health and well-being. Another finding in a systematic review by Bratman et al. (2019) is that exposure to natural environments was associated with the reduction of stress, an increase in social cohesion or physical activity and replenishment of cognitive capacities. The lack of attachment to nature and its impact on human health was most noticeable during the COVID-19 global lockdown when stern restrictions were introduced globally. The consequence of the measures was that urban dwellers were stuck in the cities and had limited opportunities to get in contact with nature. A Polish study revealed that city residents experienced high stress during this period, but outdoor activities such as being surrounded by nature, a view of greenery, and plant cultivation helped them cope with the negative emotions (Mierzejewska et al. 2023). Another interesting study was conducted in Melbourne, Australia, where researchers examined experimentally the benefits that urban trees provide to humans and wildlife. They quantified the residents' perception responses to the trees before and after a scheduled tree removal in a street and an urban park environment. They found that people's reaction was context-dependent. In the urban park where large trees were cut, people were more attached to the park and trees and they wanted to plant more trees after the treatment (Ordóñez et al. 2023). However, none of these changes were discovered in the street site where fewer and smaller trees were removed (Ordóñez et al. 2023). These results indicate that retaining large, mature, aging urban trees as long as possible is important as they support wildlife and also promote people's attachment to nature. The beneficial effects of nature on children's well-being were also reported in numerous studies. For example, a study found that those students who were surrounded by high levels of tree canopy either at home or at school experienced the greatest development of emotional and behavioural regulatory skills (Scott et al. 2018). It is important to note that although a systematic review of such studies found that nature positively influences children's mental health, additional research with more rigorous study design is recommended by the authors to confirm the relationship (Tillmann et al. 2018).

Last but not least, educating residents simultaneously is at least as important as urban habitat management measures. Without this, any kind of change in the urban management will induce resistance. In Hungary, some of the citizens are understanding and supportive towards the rare mowing interventions but negative attitude toward them was also perceived (Balázsi 2021). With the current human attitude, other negative consequences may appear from residents, such as disposing garbage into the tall grass, averse attitude toward high vegetation due to its 'untidy and messy appearance', fear from bees and so forth. On the other hand, these attitudes can be handled with education, proper communication and a collaborative approach. Environmental education includes tools, programs that support knowledge, values, awareness and skills that help people take informed actions regarding toward the environment (Ardoin et al. 2020). Ideally, this training should start at the kindergarten level and should accompany people throughout their lives. However, in contrast to the current communication and educational strategy that only focuses on the problems, it is recommended that we provide potential solutions and practices simultaneously that can be applied in everyday life. For example, a study revealed that although students tended to talk more about environmental problems after the related education, they did not suggest anything to solve these difficulties (Simsekli 2015). Focusing on the problems exclusively may result in ’there is nothing we can do’ behaviour, which is definitely avoidable if we also talk about potential solutions. Understanding the (urban) ecosystem and developing environmentally conscious behaviour can also be promoted by those initiatives that attempt to include non-scientists in science, e.g. via citizen science. Citizen science may get people closer to nature, make them understand the complexity of the ecosystems and may contribute to increased trust in science.

It is estimated that by the year 2100 the expansion of urban environment will result in the loss of additional 11–33 million hectares of natural habitats and huge natural habitat fragmentation (Li et al. 2022). It is also expected that urbanization ’will reduce local within-site species richness by 34% and species abundance by 52% per 1 km grid cell, and 7–9 species may be lost per 10 km cell’ (Li et al. 2022). However, it has to be highlighted that there are different scenarios regarding the future. According to Newbold et al. (2015), the scenario (called ’business-as-usual’ in the cited article) which is the closest to the recent trends (e.g. in emissions) gives the worst possible outcome, with the less economically developed countries experiencing the greatest biodiversity losses. In this paper, the best scenario for biodiversity would be created if definite changes were executed in land use (e.g. preservation of primary forests, improved agricultural efficiency, changes in dietary habits, decreases in cropland and pasture areas) and energy use (e.g. decline in overall energy use, decreased use of fossil fuels). However, in my personal opinion, this scenario is reachable only if the majority of humanity stands up for it and is willing to make changes in their own lives, even by going beyond their current comfort zone.

THESIS POINTS

1. I validated a frequently used method for quantifying nestling food from video recordings. I proved experimentally that measuring the length and width of artificial caterpillars on screen provides accurate, unbiased and highly repeatable data of their real size parameters. I showed that the diameter of the nest box's entrance hole can be properly used for size reference purposes. I also justified that accurate measurements can be made by multiple observers if observers are provided with a clear description of the measurement protocol.

2. In those two years of the study when markedly lower caterpillar biomass and reproductive success was reported in urban compared to forest habitats during first broods, I found that urban parents brought smaller prey items to their nestlings and provided more non-arthropod food instead of caterpillars compared to the forest parents. In contrast, in that year when there was only small difference in caterpillar biomass and reproductive success between the habitats, urban parents were able to compensate for the scarcity of caterpillars by provisioning other arthropods and delivering cc. twice as large caterpillars as in the other two years.

3. In forest habitats I found no seasonal difference in nestlings' diet, i.e. nestlings received similar composition and amount of food in seasonally first and second broods, and their body mass and survival did not differ between the broods either. Since forest parents reared fewer chicks during their second broods, these results imply that they were able to adjust their brood size to the changing local food availability and rear all hatched nestlings successfully. In contrast, urban great tits tended to bring fewer caterpillars in second compared to their first broods and I observed decreased nestling survival in urban second broods. These results suggest that urban parents are not able to adjust their brood size properly to the changing caterpillar availability in second broods.

4. Both field studies supported the food limitation hypothesis, suggesting that the reduced availability of high-quality food (caterpillars) is probably a major driver of the reduced reproductive success observed in first and second broods in the studied cities. However, our results also suggest that sometimes it is possible to catch a better year in the city when urban parents can feed their nestlings with large caterpillars and relatively more non-caterpillar arthropods rather than non-arthropod prey, which may cause detectable increase in urban birds' reproductive success. The results also highlight that long-term studies on urban populations with robust sample sizes are needed to fully understand the implications of among-year variation in environmental conditions.

TÉZISPONTOK

1. Validáltam egy olyan, gyakran használt mérési módszert, amely a fiókák táplálékának mennyiségi meghatározására szolgál. Kísérletileg igazoltam, hogy a hernyók hosszának és szélességének képernyőn történő mérése pontos, torzítatlan és nagymértékben megismételhető adatokat szolgáltat a valós méret-paramétereikről. Kimutattam továbbá, hogy az odú bejárati nyílásának átmérője megfelelően használható méretreferenciának, illetve meggyőződtem arról is, hogy a mérések több megfigyelő esetében is jól ismételhetőek, ha a megfigyelők rendelkezésére áll a mérési protokoll pontos leírása.

2. Abban a két évben, amikor a városi élőhelyeken jelentősen kevesebb hernyóbiomasszát és gyengébb szaporodási sikert figyeltünk meg, azt tapasztaltam, hogy a városi szülők kisebb zsákmányt hordtak fiókáiknak az erdei fajtársaikhoz képest, illetve a városi fiókák étrendje nagyobb részben tartalmazott nem-ízeltlábú táplálékot a hernyók helyett. Ezzel szemben abban az évben, amikor a hernyók biomasszájában és a széncinegék szaporodási sikerében nem volt jelentős élőhely különbség, a fiókatáplálékban is kisebb élőhelyi különbséget találtam. Ebben az évben a városi széncinegék képesek voltak kompenzálni a hernyók hiányát azzal, hogy más ízeltlábúakat hordtak fiókáiknak, illetve a zsákmányolt hernyók mérete több, mint kétszer nagyobb volt a többi évhez képest.

3. Erdei élőhelyeken nem tapasztaltam szezonális különbséget a fiókák étrendjében (azaz a fiókák hasonló mennyiségű és összetételű táplálékot kaptak első és másodköltések során), valamint testtömegük és túlélésük sem különbözött a költések közt. Mivel az erdei szülők kevesebb fiókát neveltek a másodköltések során, ezek az eredmények arra utalnak, hogy a szülők a fészekaljméretet hozzá tudták igazítani a hernyók szezonális változásához, így képesek voltak felnevelni közel az összes kiköltött fiókát. Ezzel szembern a városi élőhelyen azt tapasztaltam, hogy a szülők hajlamosak voltak kevesebb hernyót hordani fiókáiknak másodköltések során és a fiókáik túlélése is alulmaradt az első költésekhez képest. Ezek az eredmények arra utalnak, hogy a városi szülők nem tudják megfelelően hozzáigazítani fészekaljméretüket a hernyók szezonálisan csökkenő mennyiségéhez.

4. Mindkét terepi vizsgálat alátámasztotta a táplálék-limitáció hipotézist, tehát valószínűleg a jó minőségű táplálék (hernyók) korlátozott elérhetősége az egyik fő mozgatórugója a vizsgált városi széncinege populációk alacsonyabb szaporodási sikerének. Eredményeink azonban arra is utalnak, hogy olykor jobb évet is ki lehet fogni városban, azaz amikor a városi szülők nagy hernyóval és relatíve több ízeltlábúval etethetik fiókáikat, és így nagyobb szaporodási sikert érhetnek el. Az eredmények továbbá

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PUBLICATIONS

Publications included in the thesis

1. **Sinkovics**, **C.**, Seress, G., Fábián, V., Sándor, K. & Liker, A. (2018): Obtaining accurate measurements of the size and volume of insects fed to nestlings from video recordings. *Journal of Field Ornithology* 89(2): 165-172; IF: 1.33
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APPENDICES

Appendices to Chapter IV

Table A4.1. *Size categories of prey items. We categorized the clearly visible but non-measurable prey items according to their sizes relative to the birds' beak, as given in the 'Definition' column. The corresponding size range is given in the 'Size range' column, as estimated from the average beak sizes of the studied great tit populations (Sinkovics et al., unpublished data). Accurately measured prey items (i.e. those for that we were able to measure length and width in mm) were also classified into the same categories, and the mean length and width of these preys are given in the 'Average size' column for each category.*

Category	Definition	Thresholds by beak size	Average size
Length			
short	shorter than the beak (with at least one third of the beak length)	< 8.6 mm	6.16 mm
medium	~ beak length	8.6-17.2 mm	13.17 mm
long	longer than the beak (with at least one third of the beak length)	17.2-25.8 mm	21.19 mm
extra long	at least twice longer than the beak length	> 25.8 mm	29.12 mm
Width			
thin	thinner than the beak (with at least one third of the beak height)	< 3.2 mm	2.48 mm
medium	~ as thick as the beak	3.2-6.3 mm	4.13 mm
thick	thicker than the beak (with at least one third of the beak height)	> 6.3 mm	7.03 mm

Table A4.2. *Prey volume categories based on the size categories relative to beak length, and their estimated average volume. The average volume was estimated from subsets of preys that fell into a given category and their size could also be measured accurately (in mm) from the screenshots.*

Volume category	Average volume (mm^3)
short - thin	27.77
short - medium	82.78
short - thick	256.81
medium - thin	64.14
medium - medium	175.67
medium - thick	472.03
long - thin	121.14
long - medium	284.16
long - thick	894.15
extra long - thin	182.8
extra long - medium	454.69
extra long - thick	1173.17

***Table A4.3**. Extended models related to the amount of nestling food. Statistically significant ($p < 0.05$) differences are highlighted in bold.*

	LM model		
	DF	**χ2**	**p value**
Number of feeding visits			
Site	3	1389.2	**0.006**
Year	2	134.9	0.533
Centered date	1	97.6	0.34
Time of the day	2	234.9	0.335
Temperature	1	3.1	0.864
Site × Year	6	911.3	0.210
Feeding rate			
Site	3	37.609	**< 0.001**
Year	2	3.896	0.229
Centered date	1	0.598	0.500
Time of the day	2	0.153	0.943
Temperature	1	1.138	0.352
Site × Year	6	18.704	**0.032**
Average prey volume (mm^3)			
Site	3	77323	**< 0.001**
Year	2	71969	**< 0.001**
Centered date	1	1	0.987
Time of the day	2	4173	0.581
Temperature	1	1168	0.582
Site × Year	6	32408	0.220
Hourly prey volume (mm^3)			
Site	3	131934	0.103
Year	2	116914	0.065
Centered date	1	33102	0.209
Time of the day	2	77317	0.161
Temperature	1	155	0.931
Site × Year	6	345684	**0.017**

Table A4.4. *Extended model related to the caterpillar volume. Statistically significant (p < 0.05) differences are highlighted in bold.*

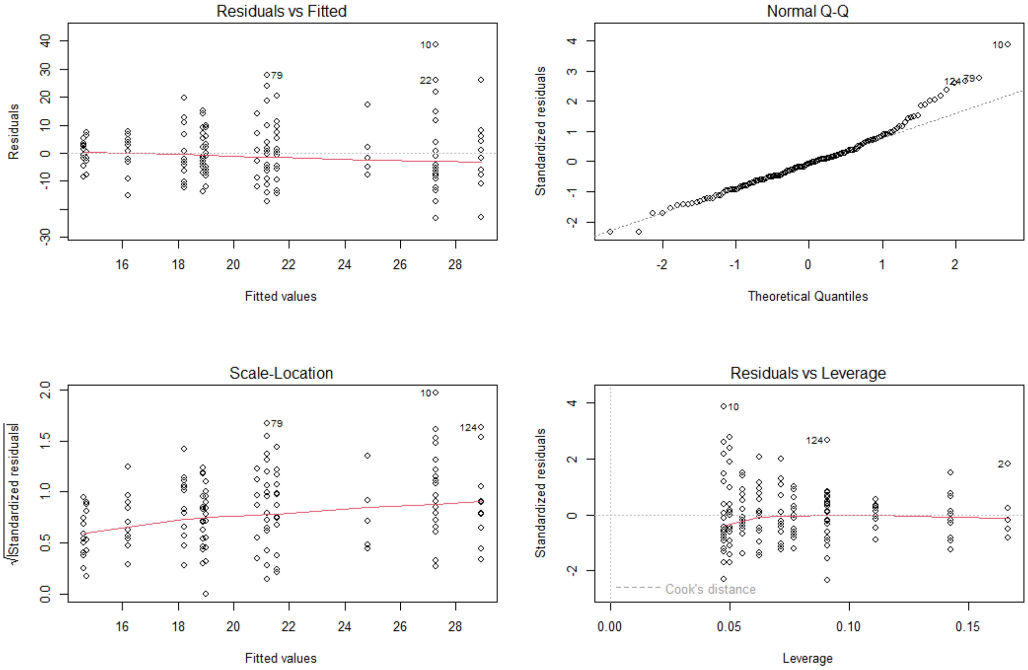
LME model			
	DF	**χ2**	**p value**
Caterpillar volume			
Site	3	18.714	**< 0.001**
Year	2	27.237	**< 0.001**
Centered date	1	0.542	0.462
Time of the day	2	1.038	0.595
Temperature	1	0.257	0.612
Site × Year	6	21.554	**0.001**

Table A4.5. *Extended models related to the composition of nestling diet. Statistically significant (p < 0.05) differences are highlighted in bold.*

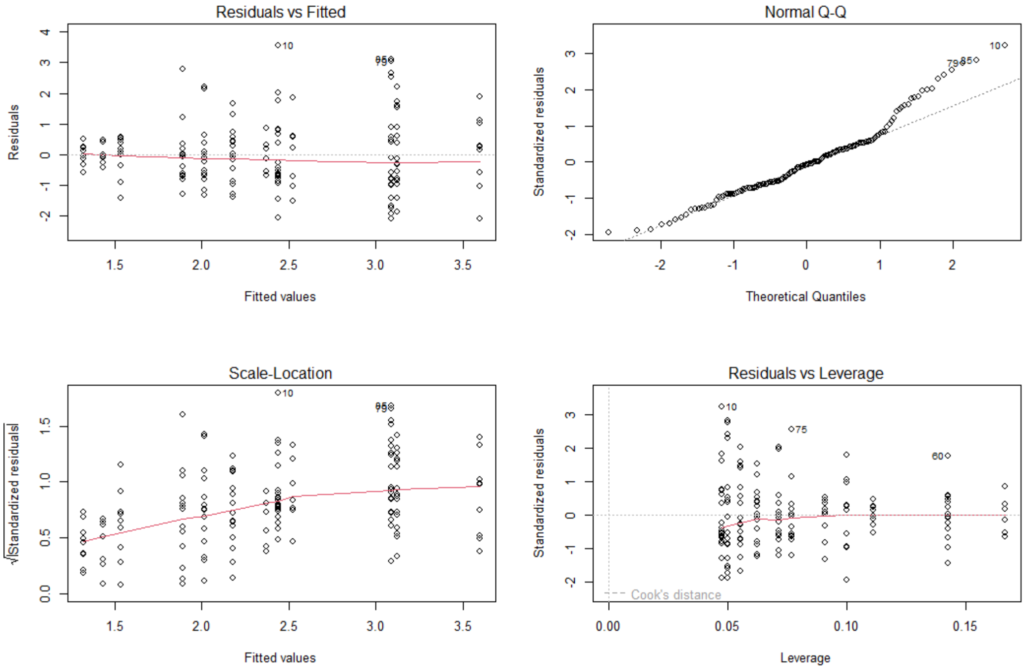
GLM model			
	DF	**χ2**	**p value**
Caterpillar vs. non-caterpillar			
Site	3	61.285	**< 0.001**
Year	2	1.292	0.524
Centered date	1	0.91	0.34
Time of the day	2	2.805	0.246
Temperature	1	0.119	0.73
Site × Year	6	17.308	**0.008**
Other arthropods vs. non-arthropods			
Site	3	25.277	**< 0.001**
Year	2	9.131	**0.010**
Centered date	1	0.133	0.715
Time of the day	2	0.585	0.746
Temperature	1	2.510	0.113
Site × Year	6	10.823	0.094

Figure A4.1. Model diagnostic plots for the final models, corresponding to Table IV.3. and Table IV.4.

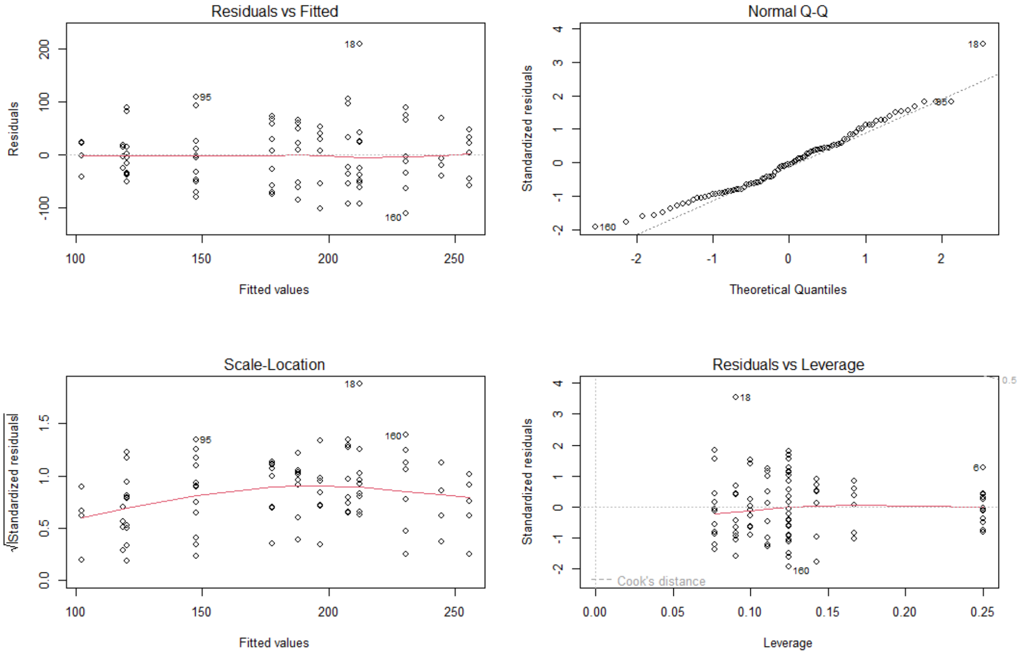
A) Number of feeding visits



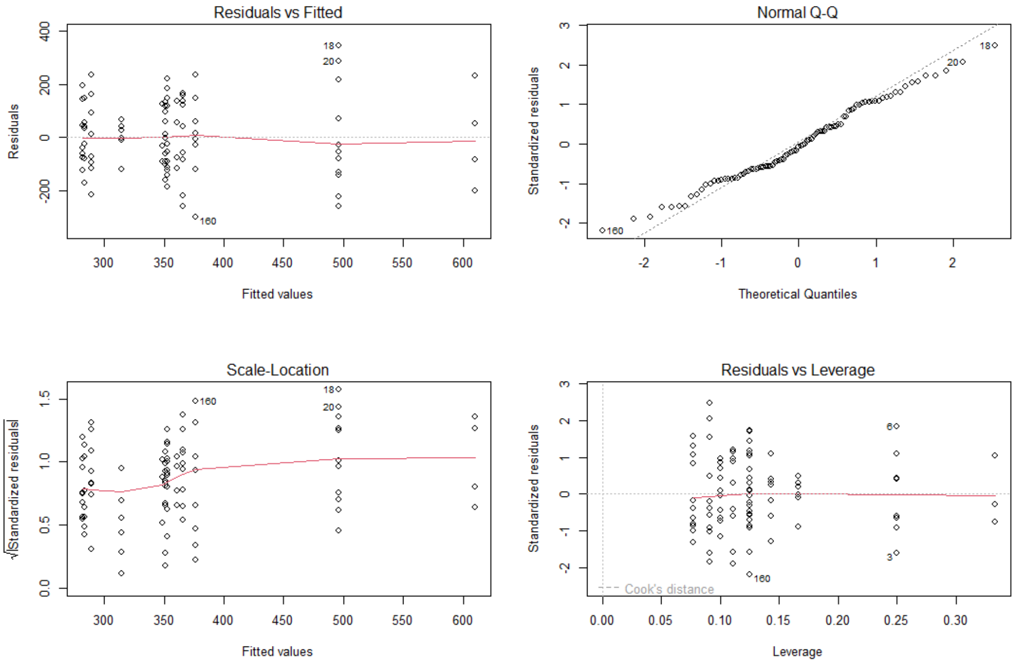
B) Feeding rate



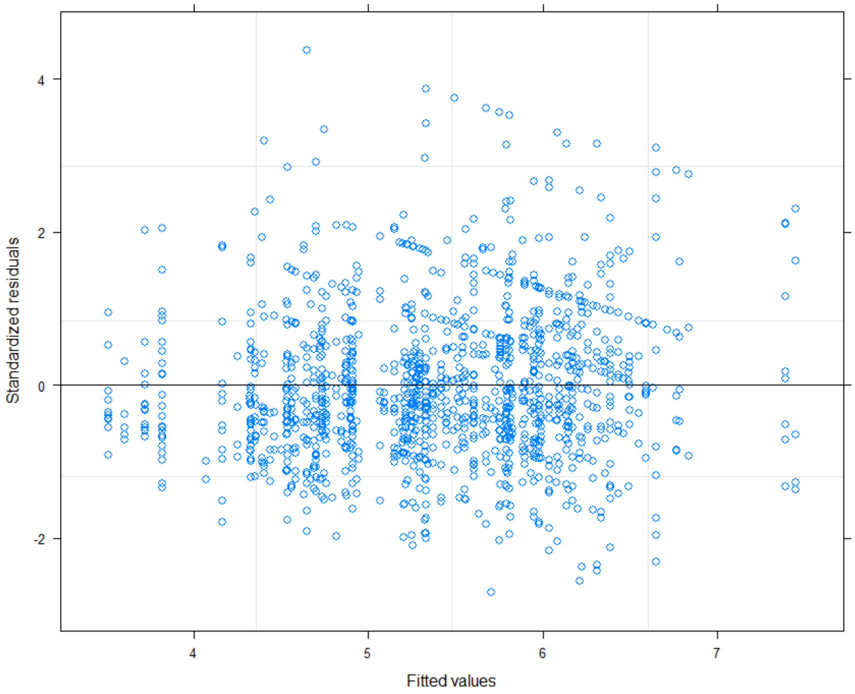
C) Average prey volume



D) Hourly prey volume



E) Caterpillar volume



Appendices to Chapter V

Table A5.1. Median and range (in brackets) hatching dates (day/month) of the video-recorded broods. The number of video-recorded broods is provided for each site (N).

	2014		2015		2016	
	First brood	Second brood	First brood	Second brood	First brood	Second brood
Szentgál	17/04 (17-18/04) N = 3	22/05 (21-25/05) N = 3	- N = 0	- N = 0	02/05 (30/04-04/05) N = 5	07/06 (06-12/06) N = 5
Vilma-puszta	21/04 (21-22/04) N = 2	27/05 (27-28/05) N = 2	- N = 0	- N = 0	- N = 0	- N = 0
Balatonfüred	14/04 (-) N = 1	30/05 (-) N = 1	14/04 (-) N = 1	30/05 (-) N = 1	14/04 (14-24/04) N = 3	28/05 (27/05-16/06) N = 3
Veszprém	13/04 (11-18/04) N = 5	03.06. (20.05-09.06.) N = 5	- (02-05/05) N = 2	- (21-25/06) N = 2	24/04 (17-28/04) N = 10	10/06 (03-21/06.) N = 10

Table A5.2. Age structure of the video-recorded parents in each habitat and site. 'Young' refers to 1-year-old parents (hatched in the previous year), 'older' refers to parents older than 2 years (i.e., having at least one breeding season before the current one). Fisher's exact test indicated no statistically significant difference between the distribution of the two age groups in the two habitat types (forest vs. urban; p = 1.000).

	Young	Older
Forest habitat	4	16
Szentgál	3	13
Vilma-puszta	1	3
Urban habitat	9	35
Balatonfüred	6	4
Veszprém	3	31

Table A5.3. Maximum brood size (mean ± SE) at each study site. Maximum brood size was estimated as the maximum number of potentially hatched nestlings in a brood (calculated as the maximum number of eggs observed in the nest minus unhatched and broken eggs).

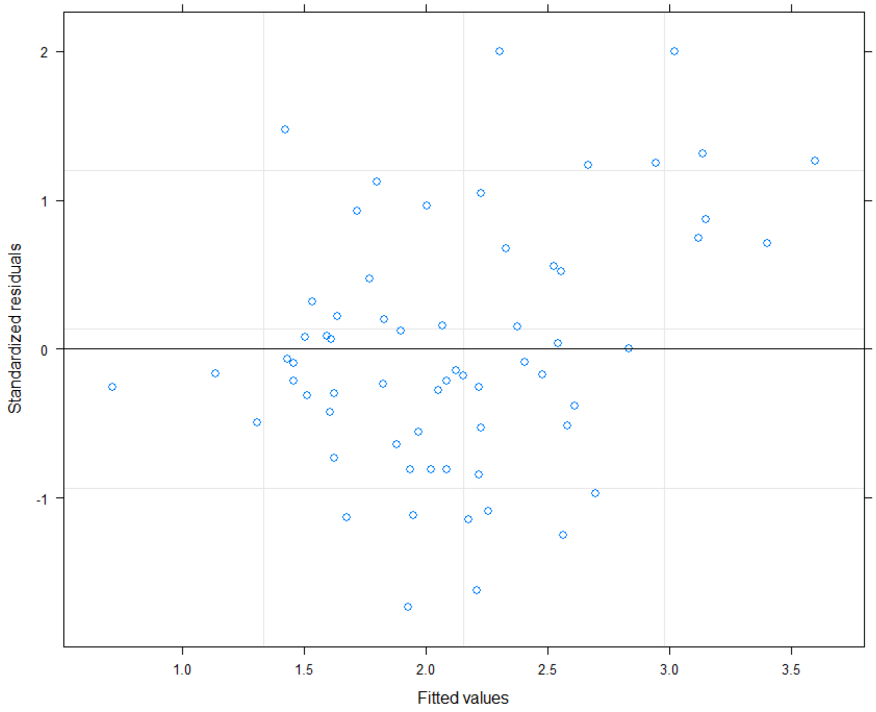
	2014		2015		2016	
	First brood	Second brood	First brood	Second brood	First brood	Second brood
Szentgál	10 ± 0.58	8.3 ± 0.67	-	-	10.8 ± 0.37	6.6 ± 1.17
Vilma-puszta	11 ± 0.00	8.5 ± 0.5	-	-	-	-
Balatonfüred	11	8	9	4	7.33 ± 1.67	6.33 ± 2.19
Veszprém	9.6 ± 0.93	8 ± 0.77	9 ± 0.00	6.5 ± 0.5	8.5 ± 0.54	6.6 ± 0.22

Table A5.4. Final models with allowing for differences in standard deviations.

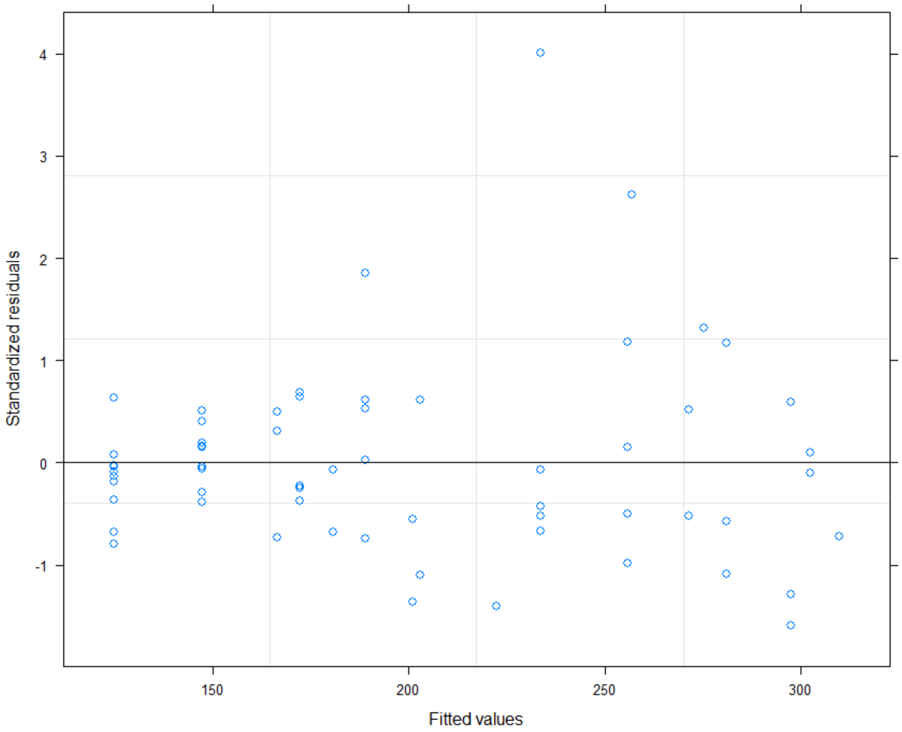
(A) GLMM/LME models				**(B) Linear contrasts between first and second broods in forest and urban habitats**			
Predictors	**DF**	**χ2**	***p*-value**	**habitat**	**contrast ± SE**	**t**	**adjusted *p*-value**
Feeding rate (LME)							
Site	3	3.246	0.355	Forest	0.211 ± 0.227	0.931	0.361
Brood type	1	6.221	**0.013**	Urban	0.319 ± 0.190	1.674	0.213
Year	2	13.338	**0.001**				
Date of observation	1	4.933	**0.026**				
Time of day	2	208.606	**< 0.001**				
Site × brood type	3	2.906	0.406				
Average prey volume (mm^3; LME)							
Site	3	1.155	0.764	Forest	-23.84 ± 38.7	-0.617	0.917
Brood type	1	0.079	0.779	Urban	7.13 ± 67.7	0.105	0.917
Year	2	12.093	**0.002**				
Site × brood type	3	0.241	0.971				
Nestlings' body mass (g)							
Site	3	17.149	**< 0.001**	Forest	1.061 ± 0.641	1.655	0.218
Brood type	1	1.667	0.197	Urban	-0.178 ± 0.435	-0.409	0.686
Year	2	9.086	**0.011**				
Site × brood type	3	4.806	0.187				

Figure A5.1. Model diagnostic plots (standardized residuals versus fitted values) for the final models, corresponding to Table V.3. and Table V.4.

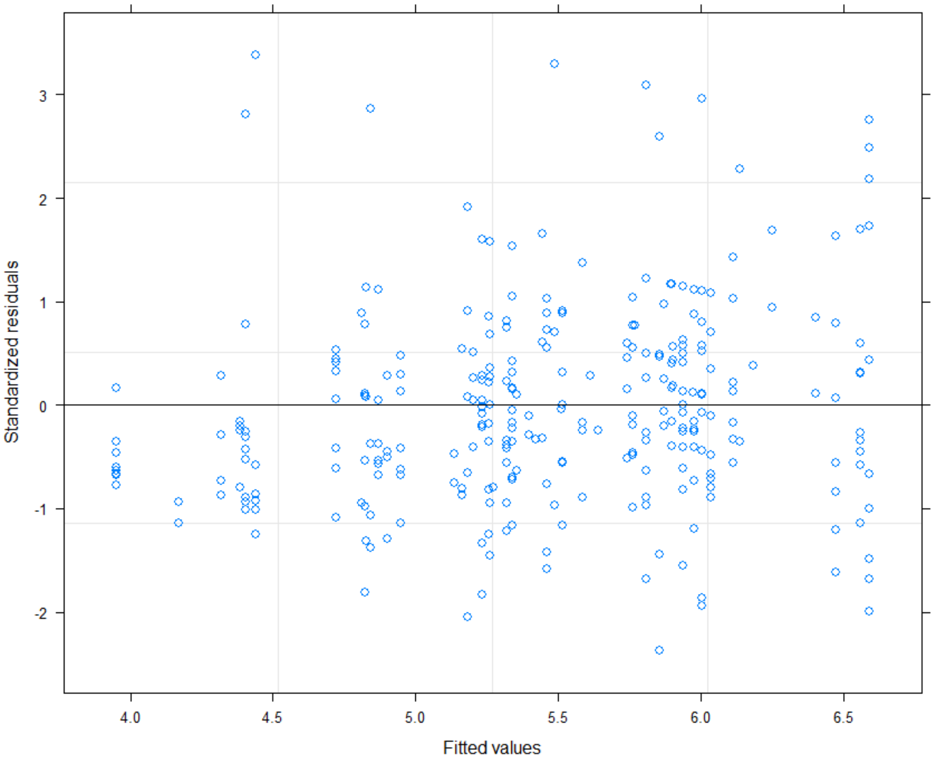
A) Feeding rate



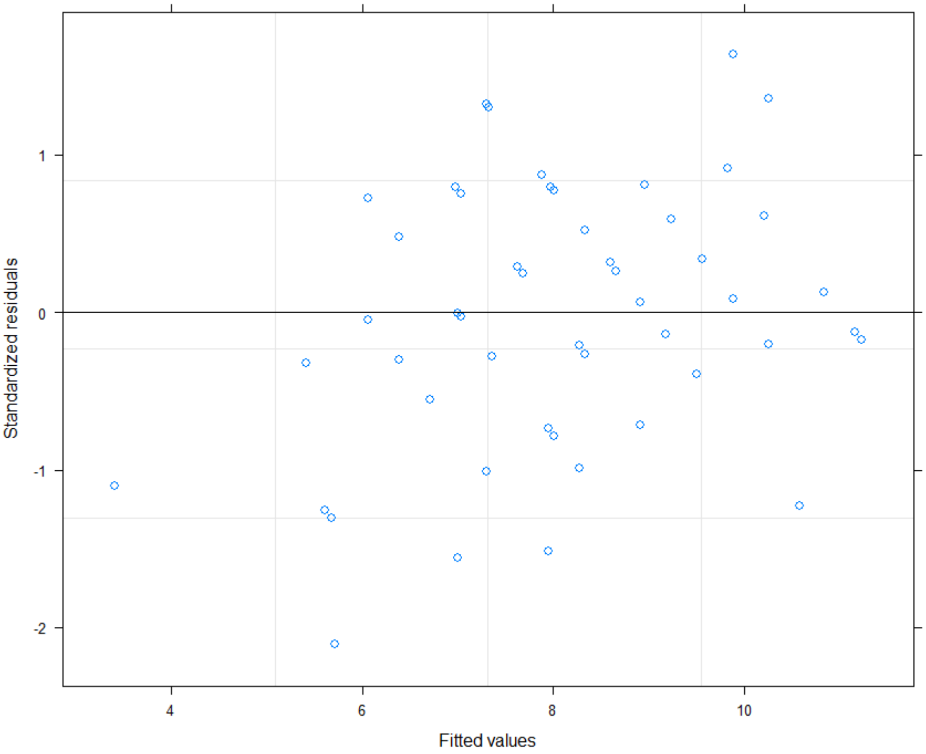
B) Average prey volume



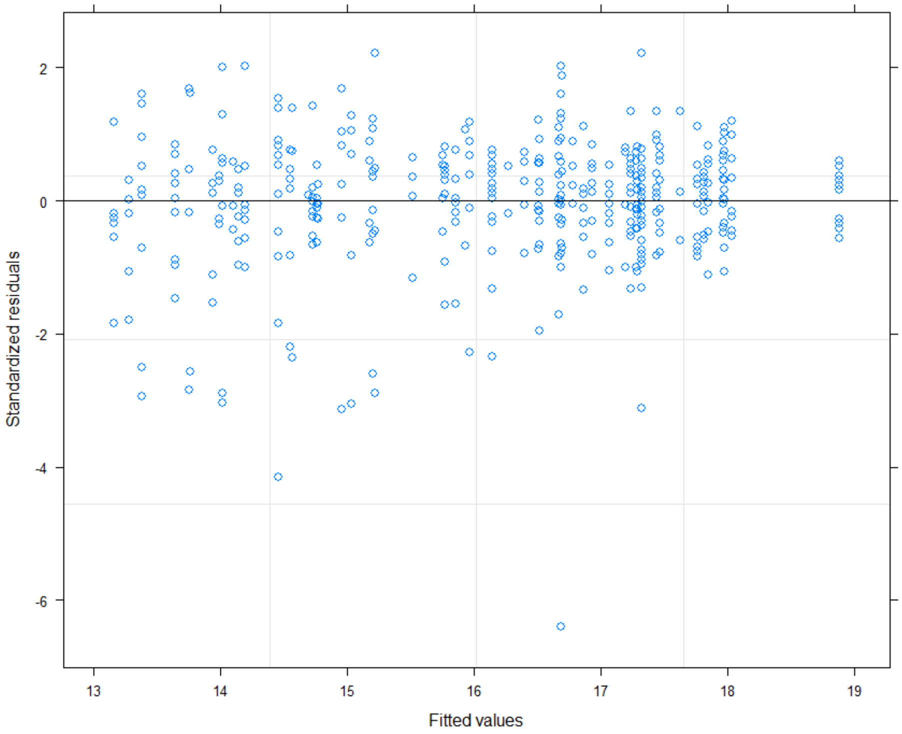
C) Caterpillar volume



D) Maximum brood size



E) Nestlings' body mass



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