



Extreme Hot Weather Has Stronger Impacts on Avian Reproduction in Forests Than in Cities

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Climate change and urbanisation are among the most salient human-induced changes affecting Earth's biota. Extreme weather events can have high biological impacts and are becoming more frequent recently. In cities, the urban heat island can amplify the intensity and frequency of hot weather events. However, the joint effects of heat events and urban microclimate on wildlife are unclear, as urban populations may either suffer more from increased heat stress or may adapt to tolerate warmer temperatures. Here, we test whether the effects of hot weather on reproductive success of great tits (*Parus major*) are exacerbated or dampened in urban environments compared to forest habitats. By studying 760 broods from two urban and two forest populations over 6 years, we show that 14–16 days-old nestlings have smaller body mass and tarsus length, and suffer increased mortality when they experience a higher number of hot days during the nestling period. The negative effects of hot weather on body mass and survival are significantly stronger in forests than in urban areas, where these effects are dampened or even reversed. These results suggest that urban nestlings are less vulnerable to extreme hot weather conditions than their non-urban conspecifics. This difference might be the result of adaptations that facilitate heat dissipation, including smaller body size, altered plumage and reduced brood size. Alternatively or additionally, parental provisioning and food availability may be less affected by heat in urban areas. Our findings suggest that adaptation to heat stress may help birds cope with the joint challenges of climate change and urbanisation.

Keywords: climate change, heatwave, urban heat island (UHI), offspring size, offspring mortality, thermal tolerance

INTRODUCTION

Current large-scale environmental changes are substantially influencing the ecological conditions for Earth's biota. Climate change is one of the dominant global processes that affect a wide range of organisms. Its effects include systematic changes in the long-term average meteorological conditions and also increases in the frequency of extreme weather events like heatwaves, droughts,

and heavy storms (Buckley and Huey, 2016; Drumond et al., 2020; Perkins-Kirkpatrick and Lewis, 2020). These climatic changes are occurring in a world that is experiencing global-scale transformation of natural habitats into heavily modified anthropogenic habitats. For example, current estimates show that 77% of the terrestrial habitats have already been modified by the direct effects of human activities such as agriculture and urbanisation (Watson et al., 2018), and the remaining pristine habitats are also disappearing at a high rate (Watson et al., 2016, 2018; Di Marco et al., 2019) forcing an increasing number of wildlife populations to persist in anthropogenic environments (Alberti and Marzluff, 2004). Although the ecological and evolutionary consequences of different global processes such as climate change and anthropogenic land-use conversion are most often investigated separately, they obviously do not act independently. Thus to better understand their current effects and to predict the changes likely induced in the future, we need to investigate their joint impacts in natural systems.

Heat events, including hot days and heatwaves, are among those extreme meteorological events that have become more frequent in the last few decades (Drumond et al., 2020). Extreme hot conditions can have strong biological impacts, affecting both survival and reproduction of organisms (Mora et al., 2017; Woodroffe et al., 2017; Conradie et al., 2019). For example, when hot days occurred for several consecutive days in Southern and Western Europe in 2003, it resulted in an estimated 70,000 heat-related human deaths (Robine et al., 2008) and was followed by detectable decreases in wild bird populations (Jiguet et al., 2006). However, even a single hot day can cause acute heat stress and have metabolic costs (Moagi et al., 2021). Extreme hot weather affects reproductive success negatively in a wide range of taxa, including both ectothermic (Zizzari and Ellers, 2011; Dayananda et al., 2017) and endothermic animals (Welbergen et al., 2008; Conrey et al., 2016; Marrot et al., 2017; Woodroffe et al., 2017; Van de Ven et al., 2020; Bourne et al., 2021; McCowan and Griffith, 2021; Oswald et al., 2021). These effects of extreme hot weather may be mediated by several, non-exclusive mechanisms, including both direct effects of heat stress on physiological and cognitive functioning (Welbergen et al., 2008; Danner et al., 2021; McCowan and Griffith, 2021) and indirect effects of heat *via* altered ecological conditions like food or water availability (du Plessis et al., 2012; Fuller et al., 2016).

Anthropogenic habitat change, especially urbanisation, is likely to interact with extreme weather events because it fundamentally alters several basic environmental conditions, including microclimate and food availability (Alberti and Marzluff, 2004; Seress and Liker, 2015). Urban heat island (UHI) refers to the generally higher ambient temperature in cities compared to the surrounding non-urban areas, which is largely generated by heat storage in buildings and sealed roads. Its intensity can be as high as +5°C in some metropolitan areas (Landsberg, 1981; Zhao et al., 2014; Central and Climate, 2021), so organisms in cities experience higher temperatures and more frequent heat events compared to organisms in non-urban areas. The UHI effect may interact with heat events in at least two ways. First, UHI can exacerbate the biological effects of extreme heat events. For example, models show that daytime temperature

in temperate-zone cities during a heat event can be higher by, on average, 2.8°C as a result of the synergistic effect between UHI and heat events (Zhao et al., 2018). Indeed, heat stress in cities can be higher during a heat event than the sum of the background UHI effect and the heat-event effect (Li and Bou-Zeid, 2013). According to these model predictions, the number of hot days is higher in urban than in non-urban areas with an additional increase in UHI resulting in increased human mortality (Li and Bou-Zeid, 2013; Rizvi et al., 2019). Similarly, animals are more likely to reach their upper limit of thermal tolerance in cities during heat events than in non-urban areas (Krause et al., 2017). Thus, urban populations may suffer a stronger reduction in survival and reproductive success than non-urban populations due to hot days (“superimposed heat and UHI effects” hypothesis).

Second, it is also possible that during long-term exposure to UHI, urban populations become adapted to higher temperatures (“adaptation to UHI” hypothesis). For example, heat tolerance (expressed as the thermal maximum where animals become unable to coordinate their motor performance) is higher in urban compared to rural populations in various ectotherm species (Brans et al., 2017; Diamond et al., 2017; Campbell-Staton et al., 2020), and these local thermal adaptations can have consequences for their reproductive success (Meineke et al., 2013; Diamond et al., 2017; Martin et al., 2021). However, endotherm species have different constraints and mechanisms for thermoregulation compared to ectotherms, as endotherms employ not only behavioural but also a variety of physiological mechanisms to regulate body temperature which have significant energetic and hydric costs (Levesque and Marshall, 2021). Although there is much less data on urban thermal adaptations in endotherms, the smaller body size of the rodent *Peromyscus maniculatus* (Guralnick et al., 2020) and reduced number of feathers in some birds (Sándor et al., 2021) in urban populations might also reflect adaptations to the UHI.

So far, only a few studies have tested the above hypotheses for joint effects of extreme hot weather events and habitat urbanisation. Their results show either additional mortality in cities in humans (Li and Bou-Zeid, 2013) or adaptation to UHI effects in water fleas (Brans et al., 2017). Importantly, there is no field study for endotherm animal populations, despite that these are the most frequent targets of conservation efforts and play crucial roles in urban ecosystems. To help fill this knowledge gap, we tested whether heat events influence avian breeding success differently in cities and forest habitats. We analysed 6 years of breeding biology data of two urban and two forest populations of great tits (*Parus major*), a small songbird that frequently breeds in both urban and forest habitats. In this species, similarly to several other birds, reproductive performance is typically lower in urban sites than in more natural areas (Bailly et al., 2016; Seress et al., 2018). We tested whether nestlings’ body mass, tarsus length, and survival are related to the number of hot days differently in urban and forest sites. According to the “superimposed heat and UHI effects” hypothesis, we expect that heat events would result in stronger negative impacts on reproduction in urban than

forest habitats. Alternatively, the “adaptation to UHI” hypothesis predicts that heat events would have reduced impact in urban than forest populations.

MATERIALS AND METHODS

Data Collection

We installed nest-boxes for great tits in an urban site (city of Veszprém 47°05′17″N, 17°54′29″E), and in two sites in natural habitats (forests near Vilma-puszta 47°05′06.7″N, 17°51′51.4″E and Szentgál 47°06′39″N, 17°41′17″E) in 2012, and additionally in another urban site (Balatonfüred 46°57′30″N, 17°53′34″E) in 2013. Urban nest-boxes are located mostly in public parks, university campuses, and a cemetery, where vegetation contains both native and introduced plant species. Forest study sites are located in deciduous woodlands, characterized by beech *Fagus sylvatica* and hornbeam *Carpinus betulus* (in Szentgál) or downy oak *Quercus cerris* and South European flowering ash *Fraxinus ornus* (in Vilma-puszta). See detailed description of study sites in Seress et al. (2018). In March 2013, we installed a WH 2080 weather station (Ambient, LLC, AZ, United States) at each study site that recorded hourly temperature (°C) data throughout the 6 years of the study.

Great tits usually raise one or two broods per breeding season. We collected data on all breeding attempts at each site from 2013 to 2018, by recording the number of eggs and nestlings in the nest-boxes every 3–4 days from March to the end of July. There were 48 to 108 nest-boxes available in each study site, and 12 to 77% of these nest-boxes was occupied by great tits during the study period (depending on the site and year). We captured parent birds using a nest-box trap 6–15 days after their first nestling had hatched. We determined parents’ sex based on their plumage characteristics and banded each bird with a unique combination of a numbered metal band and three plastic color bands. Breeding adult birds that had been color-banded on previous occasions were identified from recordings made during the nestling period by using a small, concealed video camera attached to the nest-boxes (Seress et al., 2017). In these video samples, we considered a color-banded individual to be a parent bird if it was recorded to enter the nest-box with food at least once. Close to fledging (at day 14–16 post-hatch; day 1 being the hatching day of the first nestling in the brood), we measured nestlings’ body mass with a Pesola spring balance (± 0.1 g) and tarsus length with a Vernier caliper (± 0.1 mm).

All procedures applied during our study were in accordance with the guidelines for animal handling outlined by ASAB/ABS¹ and Hungarian laws. We have all the required permissions for capturing, measuring of the birds and monitoring their breeding from the Government Office of Veszprém County, Nature Conservation Division (former Middle Transdanubian Inspectorate for Environmental Protection, Natural Protection and Water Management; permission number: 24861/2014 and VE-09Z/03454-8/2018) and from the National Scientific Ethical

Committee on Animal Experimentation (permission number: VE/21/00480-9/2019).

Data Processing

We used both the first and second annual broods of each pair in the study. We omitted broods where we could not precisely identify the nestling period due to unknown dates of hatching and/or the failure of the entire brood before hatching, and also those broods where we had gaps in the temperature data for more than 2 days during the nestling period ($n = 190$ broods). To characterize breeding success in each brood, we focused on the size and survival of nestlings. Offspring mass is a good indicator of post-fledging survival in birds (Ronget et al., 2018), so we preferred this variable over indices of “body condition” that express body mass in relation to length, because the latter indices can be inadequate for quantifying “fatness” in growing nestlings (Kraft et al., 2019).

For analysing the effects of weather on nestling size, we used the average body mass and the average tarsus length of each brood as response variables, and we included broods where at least one offspring was alive at the time of nestlings’ measuring and banding (i.e., the age of 14–16 days). Because chick size varies with age, we omitted those few broods where the nestlings were measured before or after 14–16 days of nestling age ($n = 30$); thus we had $n = 674$ broods for nestling size analyses.

For analysing the effects of weather on nestling mortality, we used broods in which at least one offspring was alive on the third day after the hatching of the first nestling. We excluded a small number of broods ($n = 7$) that failed within the first 3 days after hatching because the average interval between our nest monitoring visits was 3 days, so estimating the number of hatched chicks and their survival before the first nest check after hatching would be very uncertain. We also excluded those broods where chick mortality was likely unrelated to weather conditions ($n = 7$), i.e., occurred due to predation or human disturbance (i.e., recorded during the next observation after the occasion of capturing the parent bird on its nest). This yielded $n = 760$ broods for nestling mortality analyses, from which 385 had no chick mortality, 319 had partial mortality, and 56 had complete brood loss during the nestling period.

We calculated all weather variables (average temperature and number of hot days, detailed below) for the nestling period of each brood individually. For investigating nestling size, weather variables were calculated for the period from the day of hatching of the first chick to the day preceding the day of banding and measuring the nestlings. This sample included only broods where banding occurred at age 14–16 days (mean \pm SE: 14.04 \pm 0.03). For analysing nestling mortality, we calculated weather variables for the period from the day of hatching of the first offspring to either the day preceding the day of recording the last nestling’s death or the day preceding the day of banding and measuring the nestlings (mean \pm SE: 13.72 \pm 0.07, range: 3 – 18 days). We calculated the average temperature as the mean of hourly temperatures over the nestling period. There are several methods for quantifying extreme hot weather (Bailey and van de Pol, 2016), using various thresholds from 21 to 43°C depending on the geographic location. We calculated the number of hot

¹www.asab.org

days during each nestling period using a threshold specific to our region. To calculate a threshold for hot days, first, we defined a reference period from the earliest hatching date to the latest chick banding date recorded in our 6-year data set (pooling all sites and years), which ranged from 9th April to 15th July. Then, to estimate the typical temperatures in our geographic area during this reference period, we used a 26-years dataset from an external reference weather station located in Szentkirályszabadja, a small village near Veszprém (47°57'06" É, 17°58'10" K, ca. 9.5 – 22 km from our study sites). This weather station is maintained by the Hungarian Meteorological Service and its temperature data are available from the National Oceanic and Atmospheric Administration database², with records of air temperature every 3 h (0, 3, 6, 12, 15, 18, 21 UTC) since 1993. Using this temperature dataset, we calculated the 90% percentile of all daily maximum temperatures for the reference period from this 26-year long dataset, which was 28.7°C. Finally, we calculated the number of hot days as the number of days when the daily maximum temperature was higher than the 28.7°C threshold during the nestling period for each brood. Fixed temperature thresholds for calculating hot days are widely used in ecological and evolutionary research (Bailey and van de Pol, 2016) based on the assumption of a fixed threshold for heat tolerance in adults and offspring (Anderson, 2006; Gardner et al., 2017; Marrot et al., 2017; McCowan and Griffith, 2021). Since there is no proper information about critical thermal tolerance values for great tit nestlings, we used the 28.7°C air temperature threshold to define hot days based on the logic that temperatures above this value have been rarely experienced (i.e., less than 10 % of time) by the studied populations over the latest decades (and given the long-term trend for climate warming, such high temperatures were likely even rarer during their earlier past).

Statistical Analyses

Analysing the effects of extreme weather is challenging. Extreme events are rare by definition, so their distribution is strongly skewed (for distribution of our variable, see **Supplementary Material, Section 1**). Furthermore, weather variables are often correlated with each other and with other variables influencing reproductive success (e.g., with calendar date), so multicollinearity can be a problem in models containing multiple predictors. Statistical methods that can handle multicollinearity, such as covariance-based structural equation modelling, are less well suited for handling non-normal residual distributions and the non-independence structure of ecological data (e.g., multiple broods per pair). Therefore, here we used general and generalized linear mixed-effects (LME and GLMM) models and Akaike's information-criterion (AIC) based model selection (Burnham and Anderson, 2002) to focus on the interaction between habitat type and the number of hot days in explaining reproductive variables. Mixed-effects models can be applied appropriately to non-normal and non-independent data, while model selection based on measures of the models' total explanatory power (model fit indices, like AIC) is not sensitive to multicollinearity (Graham, 2003).

²www.ncdc.noaa.gov

All analyses were run in R (version 4.0.0) (R Core Team, 2020). First, to examine the temperature characteristics of our study sites, we compared the number of hot days and the average temperature in the nestling periods (calculated separately for each brood) between urban and forest habitats. We constructed a generalized linear model with the generalized Poisson distribution to handle overdispersion for the number of hot days using "glmmTMB" package (Brooks et al., 2017), and a linear model for the average temperatures. In both models, study site (4 sites) and year (6 years) were the predictors. To statistically compare the mean of each meteorological variable between the two habitat types, we calculated marginal means from the models for each study site, then calculated a linear contrast for habitat comparison as the difference of the average of the two urban sites from the average of the two forest sites, using the "emmeans" R package (Lenth, 2018). We used this 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 are unreliable (Piepho et al., 2003; Bolker et al., 2008), whereas including both habitat type and site as fixed effects would have resulted in strong collinearity between these two factors (Dormann et al., 2013). Instead, we treated the four sites as if they were two control groups and two treatment groups in an experiment, and we used a pre-planned comparison to test the prediction that the two treatment (i.e., urban) groups would differ from the two control (i.e., forest) groups. Such pre-planned comparisons are a powerful approach for testing *a priori* hypotheses (Ruxton and Beauchamp, 2008).

To analyse average nestling mass and average tarsus length as response variables, we used the "lme" function of the "nlme" R package (Pinheiro et al., 2013) which assumes Gaussian error. For nestling mortality (proportion of hatched chicks that died by the age of 14–16 days) as the response variable, we used GLMM models using the "glmer" function of the "lme4" R package (Bates et al., 2015) with binomial error distribution and logit link function. All of our models contained pair identity as a random factor to control for the non-independence of broods produced by the same pair. Broods got the same pair ID if both the female and the male parents were the same, and a new pair ID was assigned to the brood when it had at least one different parent. Pairs where one or both parents were unidentifiable ($n = 43$ and 139 , respectively) got separate pair IDs (see **Supplementary Material, Section 1, Supplementary Table 1** for random effect of pair ID). There were 111 pairs of parents that had more than one brood in our dataset, ranging 2–6 broods/pair. Additionally, to handle overdispersion in models of nestling mortality, we used an observation-level random effect (Maindonald and Braun, 2010) and ran the models with the BOBYQA optimizer (Bates et al., 2015).

First, we built a simple model for each of the three response variables (nestling mass, tarsus length, and mortality) including only the number of hot days (used as a numeric covariate) and study site (used as a factor with four levels), and their two-way interaction as predictors. We carefully inspected all relevant diagnostics to ensure that model fit was adequate for all models (see **Supplementary Material, Sections 2, 3**). Then, to statistically compare the effect of hot days on nestling size and

mortality between the two habitat types, we calculated the slopes of the relationship between reproductive success measurements and the number of hot days for each study population, and we compared the average of the two urban slopes with the average of the two forest slopes using a linear contrast.

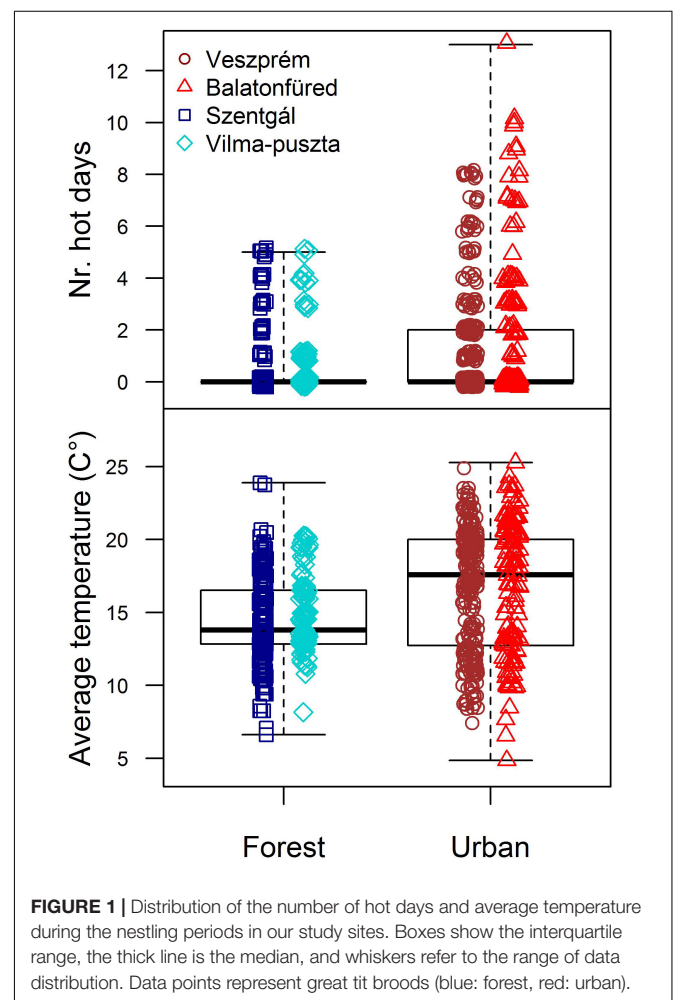
To infer the robustness of the results from the simple models, we also built multi-predictor models which included further potentially important predictor variables. In all models of our three response variables, we included year as a categorical variable, the average temperature during the nestling period and hatching date as numeric covariates, the latter defined as the number of days elapsed from the 1st January annually to the hatching of the first nestling in each brood. We also added the quadratic term of hatching date, because a preliminary inspection of diagnostic graphs suggested the possibility of non-linear seasonal changes in the response variables. For models of nestling characteristics (i.e., average body mass and average tarsus length of nestlings), we additionally included brood age (i.e., the number of days elapsed from the hatching of the first chick to the day of nestlings' measuring, ranging from 14 to 16 days), and brood size (i.e., the number of offspring alive at measuring). We standardized all numeric predictors using z-transformation for our multi-predictor analyses to avoid model convergence problems due to different scales of variables. Based on variance inflation factor (VIF), we detected high levels of multicollinearity in these multi-predictor models (see **Supplementary Material, Section 4, Supplementary Table 2**). Because multicollinearity with VIF values > ca. 2 can lead to unreliable standard errors, non-significant parameter estimates from such models must be treated with caution (Graham, 2003). Therefore, such models cannot be used for quantifying the effects of each predictor: for example, the number of hot days systematically increases with date, so the effects of hot days and other seasonal changes cannot be separated or compared by using our observational data. However, the set of predictors that yields the best explanatory power can be correctly identified by model selection based on model fit statistics (like AIC), even if multicollinearity is present (Burnham and Anderson, 2002). Therefore, we compared multi-predictor models to test if inclusion of any predictor increases model fit considerably, and then to see if our interaction of interest (urbanisation × number of hot days) is qualitatively altered by taking into account those extra predictors. We created a candidate model set for each response variable using all combinations of predictors but always including the number of hot days, study site, and their interaction (because this interaction was the focus of our study, and our goal with the model-selection procedure was to see if this interaction yields similar habitat contrasts in the multi-predictor models as alone in the simple models). The model set contained 33 models for nestling size (**Supplementary Material, Section 5, Supplementary Tables 3, 4**) and 9 models for nestling mortality (**Supplementary Material, Section 5, Supplementary Table 5**). We compared the models in each model set based on their AICc (AIC corrected for sample size) to identify the most supported model(s) for each response variable (Burnham and Anderson, 2002) using the “model.sel” function of the “MuMIn” R package (Barton, 2009). From the model(s) with superior support based

on $\Delta AICc$ and Akaike weight, we calculated the slope for each study site and the linear contrast that compares the effect of hot days between urban and forest sites the same way as from the simple models.

RESULTS

Habitat Differences in Heat Events

Great tit offspring experienced markedly different temperature characteristics in urban and forest sites during the nestling periods (**Figure 1**). The incidence of hot days occurring during the nestling period was 2.7 times greater in the cities than in the forests (urban-forest difference on log scale, controlled for year effects: mean ± SE: 0.99 ± 0.13 , $t = 7.39$, $df = 750$, $p < 0.001$; **Figure 1**). At least one hot day occurred in 179 out of 390 (45.9%) urban broods and in 77 out of 370 (20.8%) forest broods. The number of hot days ranged 0–13 in urban broods, taking up a maximum of 86.7% of the total length of individual nestling periods. In contrast, forest broods experienced only 0–5 hot days, which made up a maximum of 35.7% of the nestling period (see **Supplementary Material,**



Section 1 for further details). The highest maximum temperature was 40.1°C in urban nestling periods (in June 2013) and 33.6°C in forest nestling periods (in May 2014). Hot days were often on consecutive days during the nestling periods: there were 197 broods where at least two hot days occurred, and in 107 of these broods all hot days were consecutive (out of these 107 cases of “heatwaves,” 71 were at least 3 days long). The average temperatures within the nestling periods were significantly higher in the urban habitat (mean \pm SD: 16.62 \pm 4.29°C) than in the forest habitat (14.55 \pm 2.90°C; urban-forest difference controlled for year effects: 1.52 \pm 0.27°C, $t = 5.74$, $df = 751$, $p < 0.001$; **Figure 1**).

Effects of Hot Days on Reproductive Success

Nestling Body Mass

In the simple model where predictors were the number of hot days, study site and their two-way interaction, the effect of hot days on nestling mass differed between sites (as indicated by a significant interaction between sites and number of hot days, **Table 1**) and between urban and forest habitats (according to the linear contrast *post hoc* test comparing the effects between the two urban and the two forest populations, **Table 2**): increase in the number of hot days negatively affected nestling mass in forest broods while no such trend was present for the urban broods (**Figure 2A**). This result is consistent with the site-specific trends: the two forest populations had the most negative slopes for the relationship of nestling mass with the number of hot days, whereas the slope was flat or even positive in the two urban populations (**Supplementary Material, Section 6, Supplementary Table 6**). The habitat difference in heat effect remained significant when the analysis was restricted to the range of the number of hot days that occurred in both habitats, i.e., to broods with a maximum of 5 hot days (**Supplementary Material, Section, Supplementary Table 7**).

We also tested whether the effect of hot days persist when further potentially important variables (i.e., hatching date, year, brood size and brood age) are taken into account. We built a set of models containing various combinations of these variables in addition to the number of hot days, study site and their interaction, and we compared these models using the information-theoretic approach based on AICc. Model selection for these multi-predictor models resulted in two supported models for nestling mass ($\Delta\text{AICc} < 2$; the model with the third best fit had $\Delta\text{AICc} = 4$; **Supplementary Table 3**). The first supported model included year, brood age, and brood size besides the number of hot days, study sites, and their interaction; the second supported model contained the same predictors except brood size. Linear contrasts calculated from each of these supported multi-predictor models showed a significant overall habitat difference (**Table 2**) with a more negative effect of hot days in forest compared to urban populations (**Supplementary Table 6**), corroborating the results of the simple model.

Nestling Tarsus Length

In the simple model, the interaction between site and number of hot days was significant (**Table 1**), due to the difference

between the two urban sites, with a positive slope in one site and negative in the other (**Supplementary Table 6**). The two forest sites both showed negative relationship between the number of hot days and nestling tarsus length (**Supplementary Table 6**). The linear contrast for urban-forest difference suggested no systematic habitat difference in the effect of hot days on the tarsus length of nestlings (**Table 2** and **Figure 2B**).

Model selection for the multi-predictor model set resulted in a single supported model, which contained the number of hot days, study site, their interaction, the average temperature of the nestling period, brood age, and brood size (for the other models $\Delta\text{AICc} \geq 6.68$, **Supplementary Table 4**). The result of linear contrast comparing urban and forest slopes from this model was qualitatively identical to the result from the simple model, showing no consistent habitat difference in the effect of hot days on nestling tarsus length (**Table 2** and **Supplementary Table 6**).

Nestling Mortality

The simple model showed that the effect of the number of hot days on nestling mortality differed significantly between study sites (**Table 1**). The slope of the relationship between nestling mortality and the number of hot days was positive in all populations, being highest in one of the forest sites and lowest in one of the urban sites (**Supplementary Table 6**). The slopes also differed between urban and forest populations with a stronger effect in the latter (**Table 2** and **Figure 2C**), i.e., nestling mortality increased significantly more with the number of hot days in the forests than in the cities. The habitat difference in heat effect remained significant when the analysis was restricted to broods with a maximum of 5 hot days (**Supplementary Table 7**).

Multi-predictor model selection resulted in a single supported model, which was the full model of our model set excepting the quadratic hatching date (for the other models $\Delta\text{AICc} \geq 42.87$, **Supplementary Table 5**), containing the number of hot days, study site and their interaction, the average temperature of the nestling period, year and hatching date. The linear contrast calculated from this model showed a significantly steeper slope in forests compared to urban sites (**Table 2**), corroborating again the result of the simple model.

DISCUSSION

Our study found clear differences between urban and non-urban populations of an urban exploiter passerine species in the effects of hot days on important fitness components. Although the influence of thermal environment on fitness has been shown to vary with habitat urbanisation in ectotherms (Martin et al., 2021), our study is the first to demonstrate such habitat-dependent responses to heat stress in an endothermic animal. While UHI caused a 1.19°C higher temperature on average and there were more hot days in the cities compared to forests (**Supplementary Figure 1**), hot days affected nestling mass and survival more negatively in the forest habitat type. These results are robust, as they are based on >600 broods from 6 years and four sites, and were qualitatively unchanged by taking into account several potentially confounding factors that may differ between urban

and forest habitats, such as the start of breeding and brood size. These findings highlight that both lethal and sublethal effects of heat events (i.e., the proportion of surviving offspring and their quality in terms of body mass) can differ between urban and non-urban habitats. Although information about sublethal fitness costs of hot weather is scarce (Conradie et al., 2019), developing under hot weather conditions may have long-term consequences for fitness. Our results thus support the “adaptation to UHI” hypothesis and suggest that non-urban populations of birds (and possibly other vertebrates) are more vulnerable to extreme heat than urban populations.

Heat may affect the reproductive output of birds in at least two ways: directly through offspring physiology and indirectly through food availability. Firstly, the negative effects of hot days on offspring mass and survival may emerge due to the direct physiological consequences of heat stress. Nestlings usually cannot maintain stable body temperature in the first few days of their lives, and their metabolic processes also differ from those of adults (Price and Dzialowski, 2018) leaving them potentially more vulnerable to extreme heat than adults. The heat responses of dependent offspring are poorly known, although in birds the nestling phase seems to be the most relevant period during ontogeny regarding heat effects compared to the incubation and post-fledging periods (Marques-Santos and Dingemanse, 2020). In hot environments, individuals can less effectively dissipate the excess heat as a consequence of increased metabolic rate, leading to hyperthermia. Increasing metabolism causes decreased utilization of food and faster mobilization of energy reserves, thus it may cause lower body mass. Additionally, during heat stress, evaporative water loss is elevated as the organism tries to cool itself by evaporation to maintain body temperature in the physiologically normal range, causing dehydration (Weathers,

1972; Arad et al., 1989). Thus, increased metabolic rate and water loss both can lead to decreased body mass, as it has been shown in several bird species (Quinteiro-Filho et al., 2010; Kruuk et al., 2015; Corregidor-Castro and Jones, 2021; Oswald et al., 2021). Although parents can help their nestlings thermoregulate, great tits cannot shade their nest-boxes and they are not known to be able to cool their nestlings in other ways such as providing water.

These direct physiological effects of heat might be better tolerated by urban animals due to changes in their physiological and morphological characteristics. For example, we found in the same study populations that urban great tit nestlings have fewer feathers and increased bare body surfaces than forest nestlings (Sándor et al., 2021), which may facilitate heat dissipation. Reduced body size may also help to cope with the heat in cities because animals with smaller size have a higher surface-biomass ratio which facilitates heat loss. Bergmann’s rule (Bergmann, 1847) predicts that reduced size is beneficial against dehydration and overheating in warmer environments (Weathers, 1972; but see Whitfield et al., 2015) such as cities. This idea is supported by urban-rural comparisons of invertebrate communities (Merckx et al., 2018), as well as by a study of water flea populations which found that urban individuals were generally smaller than rural ones, and smaller individuals were more heat tolerant (Brans et al., 2017). In birds, a study of white-browed scrubwrens (*Sericornis frontalis*) also found that smaller individuals survived better when more extreme hot and dry events occurred (Gardner et al., 2017). Urban birds are usually smaller than their non-urban conspecifics (Liker et al., 2008; Chamberlain et al., 2009; Caizergues et al., 2021) and this is also the case with the great tits in our study populations (Seress et al., 2018). Although experimental evidence shows that low availability of nestling food is a major cause of the reduced size of urban great tit nestlings

TABLE 1 | Relationship between the number of hot days during nestling development and nestlings’ body mass, tarsus length, and mortality, according to the simple models.

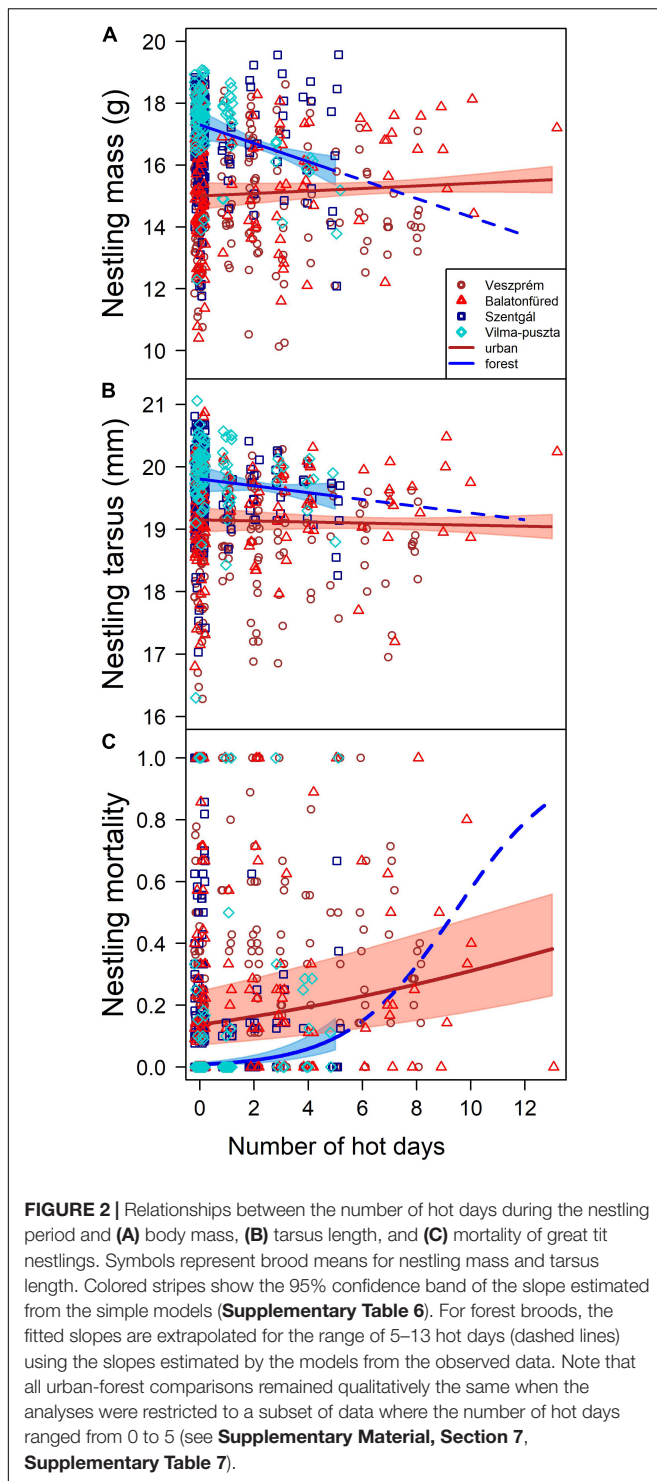
Model terms	Nestling mass			Nestling tarsus length			Nestling mortality		
	χ^2	df	p	χ^2	df	p	χ^2	df	p
Nr. hot days	3.119	1	0.077	6.134	1	0.013	5.799	1	0.016
Study site	243.518	3	<0.001	103.380	3	<0.001	91.078	3	<0.001
Nr. hot days × study site	29.289	3	<0.001	9.555	3	0.023	11.844	3	0.008

Type 3 ANOVA (analysis of deviance) table is shown for each model. Significant effects ($p < 0.05$) are highlighted in bold. For average nestling mass and tarsus length, the number of pairs was 535 and the number of broods was 674. For nestling mortality, the number of pairs was 600 and the number of broods was 760.

TABLE 2 | Differences between urban and forest habitats in the effect of hot days on nestling’s body mass, tarsus length, and mortality.

Response	Simple model				Multi-predictor model			
	contrast ± SE	df	t	p	contrast ± SE	df	t	p
Nestling mass	0.338 ± 0.085	135	3.978	<0.001	0.656 ± 0.166 / 0.720 ± 0.165	127 / 129	3.941 / 4.355	<0.001 / <0.001
Nestling tarsus length	0.046 ± 0.039	135	1.187	0.237	0.044 ± 0.075	127	0.590	0.556
Nestling mortality*	-0.408 ± 0.159	156	-2.564	0.010	-0.643 ± 0.281	149	-2.288	0.022

The table shows linear contrasts comparing the average slope of two urban versus two forest sites, calculated from the estimates of the simple models (left) and the most supported multi-predictor models (right) for each response variable. For nestling mass, results of two supported multi-predictor models are separated by “/”. Positive contrasts mean more positive slopes (i.e., less negative effects of hot days) in the urban habitat. Significant habitat differences ($p < 0.05$) are highlighted in bold. * Estimates for nestling mortality are on the logit scale.



(Seress et al., 2020), selection for better heat tolerance might also contribute to it. Finally, life-history changes may also help animals to cope with the direct effects of urban heat. For example, urban birds usually have smaller clutch size than forest birds (Chamberlain et al., 2009), which is also typical in our study populations (Seress et al., 2018, 2021). Smaller clutch size may

also be advantageous for heat dissipation when environmental temperature is high because fewer offspring produce less heat and have more space to maintain distance in the nest, which helps better heat conduction.

Secondly, indirect effects may also contribute to lower body mass and higher mortality in response to heat events. For example, hot weather may reduce food availability for insectivorous nestlings by affecting their parents and/or their prey. Caterpillars are the main source of nestling diet in great tits and many other birds, and increasing temperature strongly decreases the time to pupation in several lepidopteran species (Kingsolver et al., 1997; Lee and Roh, 2010; Lemoine et al., 2015), so optimal caterpillar food may be available for a shorter time in hot periods. Moreover, the growth of caterpillars declines rapidly above a critical temperature (Kingsolver et al., 1997) and their mortality increases when temperature is constantly high (York and Oberhauser, 2002; Lee and Roh, 2010). These heat effects may not only result in less food for nestlings but may also contribute to dehydration because caterpillars are the most water-rich items in the diet of nestlings (Zandt, 1997). These effects might be stronger in forests where the amount of available caterpillar prey is much higher in general (Seress et al., 2018) and the vast majority of nestling diet consists of caterpillars. In such environments, it might be more difficult for parent birds to compensate for a reduction in caterpillar biomass compared to cities, where nestlings are usually fed a greater proportion of other food types (Pollock et al., 2017; Jarrett et al., 2020). Water loss due to the combined effects of heat and reduced caterpillar availability might also be better compensated for in urban habitats if water is more accessible there, for example from public or garden ponds, bird water feeders, or puddles left behind after lawn irrigation. In our study, the nest-box colony in Balatonfüred is situated at ca. 700 m from Lake Balaton, and there is a small pond near some of our urban nest-boxes in Veszprém study site, while we are not aware of any permanent water sources in the forest study sites. However, we have no information on whether and how frequently the supplementary water sources are used by urban birds. Additionally, the foraging activity of parents may also decrease when temperature is high (Wiley and Ridley, 2016; Nilsson and Nord, 2018; Oswald et al., 2021), resulting in less food delivered to the offspring, and this effect might also be diminished in urban populations if parent birds have adapted to tolerate heat better (see above), or when they have more access to water than in non-urban forests. Further studies are required to test whether heat affects parental care differentially in urban and non-urban habitats.

Adaptation to constantly warmer urban environments may be achieved by microevolution, epigenetic changes, and/or phenotypic plasticity (Zhu et al., 2021). In some ectotherm species, artificial thermal selection, reciprocal transplant and common garden experiments have revealed that one or more of these mechanisms can play a role in the increased upper thermal tolerance of urban populations (Calosi et al., 2008; Brans et al., 2017; Campbell-Staton et al., 2020; Martin et al., 2021). To our knowledge, no such experiments have yet been done to identify the mechanisms of higher thermal tolerance in urbanised birds or other endothermic animals, which is an important knowledge

gap in our understanding of urban adaptations. Such experiments are also needed for quantifying the relative importance of heat *per se* and other environmental effects that may change over the season and may differ between urban and non-urban habitats, including parental investment and the availability of food and water, which was not possible with our correlative data here. Therefore, there is a great need for further studies that explore the differences in thermal tolerance between different habitats to understand how wild animals are affected by, and may adapt to, the interacting challenges of climate change and urbanisation in the Anthropocene.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be available from the authors upon request.

ETHICS STATEMENT

The animal study was reviewed and approved by the Government Office of Veszprém County, Nature Conservation Division (former Middle Transdanubian Inspectorate for Environmental Protection, Natural Protection and Water Management; permission number: 24861/2014 and VE-09Z/03454-8/2018), and the National Scientific Ethical Committee on Animal Experimentation (permission number: VE/21/00480-9/2019).

AUTHOR CONTRIBUTIONS

IP, VB, and AL designed the study, did the statistical analyses, and wrote the manuscript. IP and VB made the data visualization. All authors collected data in the field and took part in finalizing the manuscript.

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SUPPLEMENTARY MATERIAL

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