Articles

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

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

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

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

Several reasons have been proposed for the reproductive failure of urban sparrows. First, nestlings require an arthropod diet, and parents may be unable to find nestling food of sufficient quantity and/or quality due to the scarcity of native vegetation. Recent development of cities often results in losses of green space such as gardens being replaced by paved parking lots (Shaw et al. 2008), and even existing vegetation may harbor poor insect fauna if it consists mainly of exotic or evergreen plants (Southwood 1961). Supporting this view, a study in and around the city of Leicester, Britain found that the survival of sparrow

nestlings correlated negatively with high amounts of vegetable material in their diet and positively with high abundance of aphids around the nest (Peach et al. 2008). Second, arthropod density may be reduced in cities by environmental pollution, especially traffic emissions (Summers-Smith 2007). Although the effects of traffic-related air pollutants on animals are not well understood, they may affect invertebrates (Raupp et al. 2010, Zvereva and Kozlov 2010); furthermore, they might also have direct adverse impact on vertebrates such as the nestlings and adult birds (Eeva et al. 2003, Swaileh and Sansur 2006). The Leicester study also found reduced nestling growth in areas with high nitrogen-dioxide air pollution (Peach et al. 2008). Third, urban parents may suffer increased mortality by collisions with vehicles (Heij and Moeliker 1990) or predation by the growing numbers of domestic cats (Woods et al. 2003) and urbanizing raptors (Bell et al. 2010). Moreover, increased predator density may reduce the breeding success of house sparrows via indirect, sublethal effects such as decreased foraging efficiency (Beckerman et al. 2007) and impaired reproductive capacity due to physiological stress (Boonstra et al. 1998).

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

In the present study, our aims were four-fold. First, we assessed the status of the house sparrow population in a central European country, Hungary by studying temporal trends between 1999 and 2011. Second, we investigated the species' breeding success and nestling growth in differently urbanized habitats. Third, we observed the parents' chick-feeding behavior to compare the quantity and quality of nestling food between habitats. Finally, we conducted two experiments to assess the importance of environmental conditions during nestling development. In a common garden experiment we allowed adult sparrows from urban and rural sites to reproduce in the same environment in captivity, to see if they show any difference in parental qualities. If urbanization exerts long-term negative effects on adult birds (e.g. infertility, maternally derived toxins), we expect

these to manifest in the common environment as well. In the second, cross-fostering experiment we swapped few days-old nestlings between suburban and rural nests, thereby separating genetic and pre-natal environmental effects from those of the rearing environment. If urbanization mainly affects nestlings by the actual environmental conditions (e.g. diet) experienced between hatching and fledging, we expect nestling growth to be influenced by rearing habitat to a greater extent than by birth habitat.

Methods

Population trends

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

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

Reproduction and nestling growth in the field

We studied free-living house sparrows breeding in rural and suburban nests in 2009–2010. Rural nests were monitored at two farm sites (Szentgál and Vilmapuszta; Table 1, Fig. 1) and at the edges of two small villages (Hidegkút and Hárskút; Table 1, Fig. 1); these sites are characterized by

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

| Study site	Mean vegetation density score	Mean building density score	Number of cells with road	Number of cells with high (> 50%) vegetation density	Number of cells with high (> 50%) building density	Data set
Budapest, Kőbánya-Kispest 47°27'43"N, 19°09'00"E	1.03	1.15	93	11	37	CG
Veszprém, Hotel 47°05'29"N, 17°54'43"E	1.15	1.33	98	19	37	CG
Veszprém, Zoo 47°05'32"N, 17°53'43"E	1.80	0.75	58	80	17	F, CF
Nemesvámos 47°03'16"N, 17°51'52"E	1.71	0.49	27	75	11	CG
Üllő, Dóramajor 47°20'43"N, 19°19'16"E	1.97	0.35	26	97	1	CG
Hidegkút 46°59'57"N, 17°49'45"E	1.95	0.21	18	95	1	F
Szentgál 47°06'08"N, 17°42'20"E	2.00	0.03	20	100	0	F, CF
Hárskút 47°11'09"N, 17°47'53"E	2.00	0.12	12	100	0	F
Vilmapuszta 47°05'05"N, 17°52'03"E	2.00	0.06	0	100	0	F
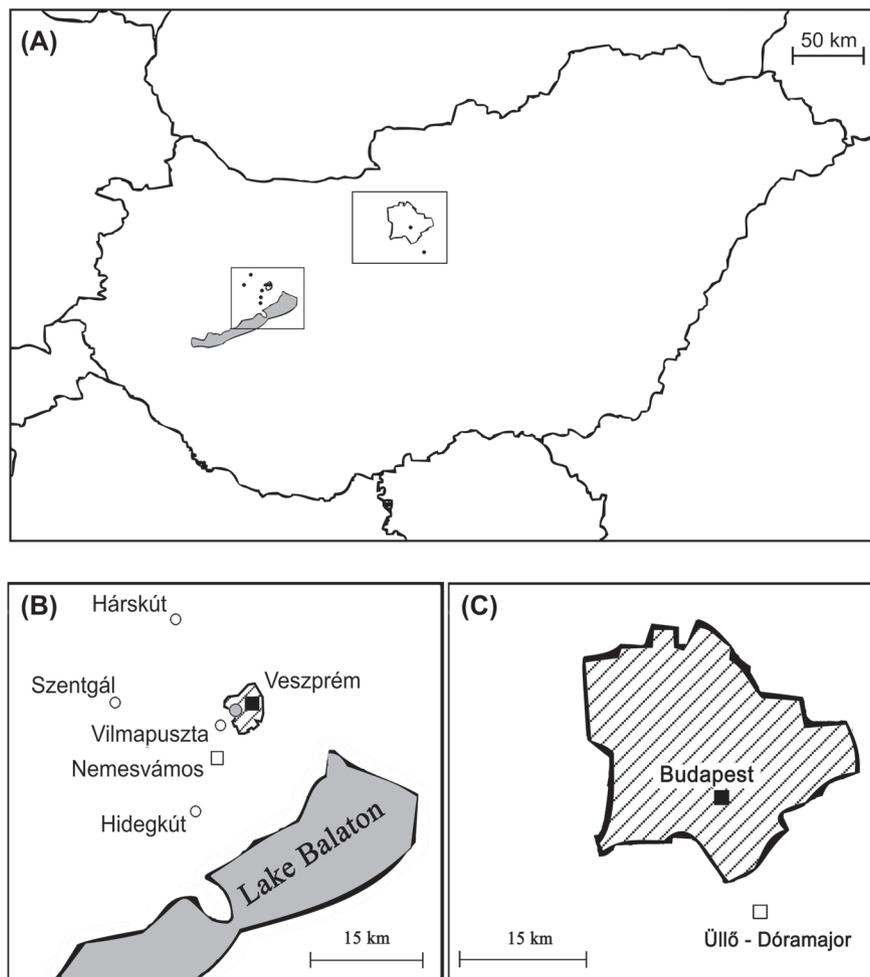
Figure 1. Locations of the study sites in Hungary. Dots represent sites of the field study and cross-fostering experiment, whereas squares represent the capture sites of birds in the common garden experiment. Rural, suburban, and urban sites are marked by white, grey, and black symbols, respectively.

high vegetation density with a few buildings and roads. Sparrows at these sites breed both in nest boxes and other available nesting sites (e.g. roofs). Suburban nests were monitored in Veszprém, in the territory of Veszprém Zoo (Table 1) which is situated at the edge of the town, directly connected to a residential area with mostly large blocks of houses and roads with moderate to heavy traffic. This site is characterized by more buildings and paved surfaces than the rural sites (Table 1) and a high level of human disturbance due to intensive daily maintenance and construction work and large visitor numbers (ca 700–2000 people d^{-1} from April to August). Furthermore, the zoo site is similar to suburban and urban sites in that its vegetation consists mostly of ornamental, evergreen and exotic species such as *Pinus nigra*. Here we studied sparrows using nest boxes; our data from earlier years at this site showed that natural and box nests did not differ in brood size (median = 3 in both types of nest, χ^2 test: $\chi^2_5 = 3.81$, p = 0.577, n = 71 nests) or nestling size (body mass: 23.61 ± 0.44 vs 23.45 ± 0.34 g, $t_{222} = 0.30$, p = 0.768; tarsus length: 18.52 ± 0.10 vs 18.46 ± 0.09 g, $t_{215} = 0.49$, p = 0.625). We could not study inner-city nests because these were not accessible and urban sparrows did not occupy the nest boxes we had provided (as in Peach et al. 2008). The mean distance between our study sites was 12.5 ± 1.5 km in a range of 2.2–20.5 km (Fig. 1). Given that the house sparrow is a very sedentary species (Anderson 2006, Liker et al. 2009, Vangestel et al. 2010, 2011) our sites were supposed to be far enough from each other to prevent significant exchange of sparrows amongst them.

We verified in two ways that our suburban site represents a more urbanized habitat for house sparrows than our rural sites. First, we quantified the degree of habitat urbanization following Liker et al. (2008) by scoring vegetation cover, building density, and the presence of paved roads in 100 cells of a 1 km² area around the center of each site (Table 1). The number of cells with high (>50%) vegetation density was less, whereas the number of cells with roads and high (>50%) building density was higher in the suburban habitat than in the rural habitats (Table 1; χ^2 tests: $\chi^2_1 > 15.74$, p < 0.001). Second, we compared the morphology of adult birds captured in autumn with mist-nets between the Veszprém Zoo and Szentgál (i.e. the site at which 91% of our rural nests were studied). In accordance with our earlier result that sparrows are smaller in more urbanized habitats (Liker et al. 2008), we found that birds at our suburban site had on average 0.93 ± 0.27 g less body mass ($t_{1023} = 3.49$, p < 0.001) and 1.18 ± 1.52 mm shorter tarsi ($t_{961} = 7.81$, p < 0.001) than birds at the rural site.

During both years, we checked all nests regularly at least twice a week from April to August (i.e. the breeding season of house sparrows in Hungary) to record the dates of laying and hatching, and the number of eggs and chicks in the nests. We measured the body mass (± 0.1 g), tarsus length (± 0.1 mm), and wing length (± 1 mm) of nestlings when they were 8–12 d old (75% of the nestlings were measured at 9–11 d of age). Brood size at this age is a good predictor of recruitment rate in house sparrows (Schwagmeyer and Mock 2008); since disturbing nests with older nestlings can cause premature fledging, we used the number of nestlings

at the time of measuring (i.e. pre-fledging age) as proxy for the number of fledglings. Nestling measurements were taken by two persons with high inter-person repeatability.

In 2010 we observed the parents' chick-feeding activity at 10 suburban and 26 rural nests between 8:00 and 14:00 when the nestlings were 5–6 (in a few cases 7–8) d old. We observed the nests from a distance either by spotting scope or by video-camera for 30 min, and recorded the number of visits by each parent. For each visit we categorized the size of food item delivered by the parent as small, medium, large or unknown following Schwagmeyer and Mock (2008) who found that the delivery rate of large food items (enormous prey or 'e-prey') strongly predicted nestling mass and recruitment in house sparrows.

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

Manipulations of the rearing environment

Common garden experiment

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

During the breeding seasons (March–August) of 2008 and 2009, birds were supplied plenty of nesting material

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

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

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

Cross-fostering experiment

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

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

Data analysis

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

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

between aviaries in any measure of reproductive success or nestling size (LME: all p > 0.163).

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

Results

Population trends

The TRIM analysis indicated a significant, moderate decline of the house sparrow in Hungary (b ± SE = −0.022 ± 0.008, p < 0.01) during the studied period

(Fig. 2). This country-wide decline was paralleled by a decrease in nest box occupancy and total number of fledglings produced per year at our suburban study site in 2005–2010, over 6 yr of the studied period (Fig. 2).

Reproduction and nestling growth in the field

Median clutch size was 5 eggs in both habitats and both years (Table 2). Hatching success was not different between rural and suburban nests (Table 2); median number of hatchlings was 4 in both habitats and both years. In contrast, the number of nestlings before fledging was significantly higher in rural than in suburban nests (Table 2, Fig. 3), and broods in both habitats were larger in 2009 than in 2010 (habitat × year interaction: p = 0.671; Table 2, Fig. 3). Thereby fledging success was higher in rural than in suburban nests and in 2009 than in 2010 (habitat × year interaction: p = 0.146; Table 2). The number of broods raised successively in a given nest was similar in both habitats in both years (Table 2).

Suburban nestlings had significantly smaller body size at the same pre-fledging age than rural nestlings (Table 2, Fig. 4): the former had on average ca 4 g less weight, 0.7 mm shorter tarsi and 2 mm shorter wings than the latter. The difference between suburban and rural habitats was similar in the two years for body mass and wing length, but it tended to be greater for tarsus length in 2010 (Table 2, Fig. 4).

The summed chick-feeding rates of males and females in 2010 did not differ significantly between suburban nests (1.15 ± 0.32 visits per nestling per 30 min) and rural nests (0.81 ± 0.12; Table 2). Analyzing the sexes separately yielded the same result. 'E-prey' was delivered in 13 out of 36 nest observations (Table 3), typically only once during 30 min. Nevertheless, 'e-prey' comprised a greater proportion of delivered food items in rural than in suburban nests (Fisher's exact test: p = 0.018, odds ratio = 0.099; Table 3).

Manipulations of the rearing environment

Common garden experiment

In the aviaries in 2008, nestlings of urban pairs had similar body mass prior to fledging (18.14 ± 3.77 g, n = 10 nestlings
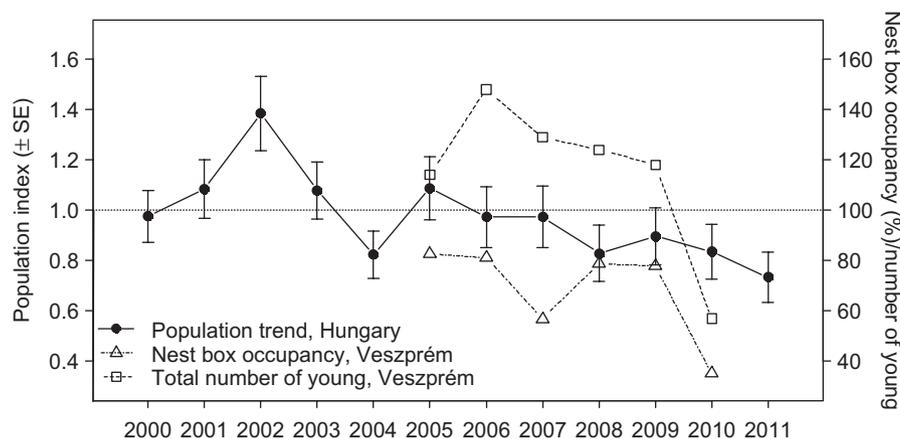

Figure 2. Temporal trends in house sparrow population size in Hungary. Population index refers to the difference in population size between the given year and the starting year of the monitoring scheme (1999; marked by a dotted line). Nest box occupancy and total number of young are shown for the suburban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

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

	b ± SE	p	Cohen's d (CI)
Clutch size[1]			
year	−0.017 ± 0.034	0.609	−0.10 (−0.47; 0.27)
habitat	0.006 ± 0.034	0.865	0.03 (−0.34; 0.41)
Hatching success[2]			
year	0.061 ± 0.060	0.313	0.16 (−0.15; 0.46)
habitat	0.075 ± 0.060	0.219	0.19 (−0.11; 0.49)
Pre-fledging brood size[3]			
year	−0.24 ± 0.104	0.024	−0.48 (−0.92; −0.07)
habitat	−0.352 ± 0.106	0.001	−0.7 (−1.15; −0.27)
Fledging success[4]			
year	−0.208 ± 0.098	0.036	−0.45 (−0.89; −0.03)
habitat	−0.3 ± 0.099	0.003	−0.64 (−1.09; −0.22)
Number of broods per nest site[5]			
year	−0.078 ± 0.093	0.406	−0.16 (−0.55; 0.22)
habitat	0.043 ± 0.097	0.657	0.09 (−0.30; 0.47)
Nestling body mass[6]			
year	−1.649 ± 0.665	0.015	−0.51 (−0.94; −0.1)
habitat	−4.381 ± 0.691	<0.001	−1.3 (−1.81; −0.84)
Nestling tarsus length[7]			
year	0.598 ± 0.276	0.033	0.46 (0.05; 0.88)
date	0.009 ± 0.003	0.003	0.62 (0.21; 1.06)
brood size	0.185 ± 0.077	0.021	0.51 (0.1; 0.94)
age	0.22 ± 0.075	0.004	0.62 (0.2; 1.06)
habitat	−0.709 ± 0.326	0.032	−0.46 (−0.89; −0.05)
habitat × year	−0.955 ± 0.482	0.051	−0.42 (−0.84; −0.01)
Nestling wing length[8]			
year	−1.403 ± 0.871	0.111	−0.33 (−0.75; 0.07)
age	3.289 ± 0.325	<0.001	2.1 (1.56; 2.74)
habitat	−2.249 ± 0.941	0.019	−0.5 (−0.93; −0.09)
Parents' feeding rate[9]			
date	−0.014 ± 0.007	0.047	−0.79 (−1.66; −0.03)
parent's sex	−0.416 ± 0.235	0.084	−0.69 (−1.53; 0.07)
habitat	0.332 ± 0.277	0.240	0.46 (−0.28; 1.27)

[1]Intercept: 1.56 ± 0.03; n = 196 broods at 115 nest sites.
[2]Intercept: −0.32 ± 0.06; n = 173 broods at 108 nest sites.
[3]Intercept: 1.31 ± 0.09; n = 146 broods at 93 nest sites.
[4]Intercept: −0.08 ± 0.09; n = 146 broods at 93 nest sites.
[5]Intercept: 0.43 ± 0.09; n = 109 nest sites.
[6]Intercept: 25.03 ± 0.60; n = 455 nestlings from 137 broods at 98 nest sites.
[7]Intercept: 14.43 ± 0.93; n = 453 nestlings from 136 broods at 97 nest sites.
[8]Intercept: 11.00 ± 3.61; n = 436 nestlings from 133 broods at 97 nest sites.
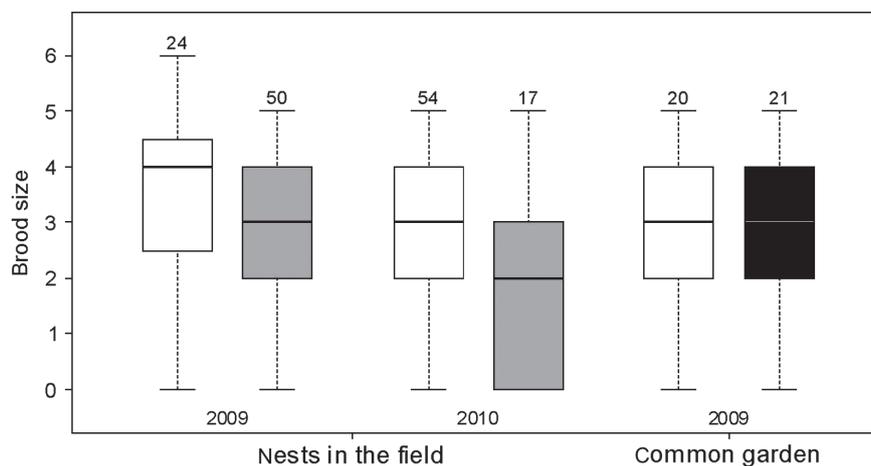[9]Intercept: 1.40 ± 0.27; n = 36 broods at 31 nest sites.

Figure 3. Brood size before fledging in rural (white) and suburban (grey) nests in the field, and by pairs from rural (white) and urban (black) habitats in the common garden experiment in 2009. Number of nests is shown above each boxplot. Medians, interquartile ranges and data ranges are shown by the middle thick lines, the boxes, and the whiskers, respectively.
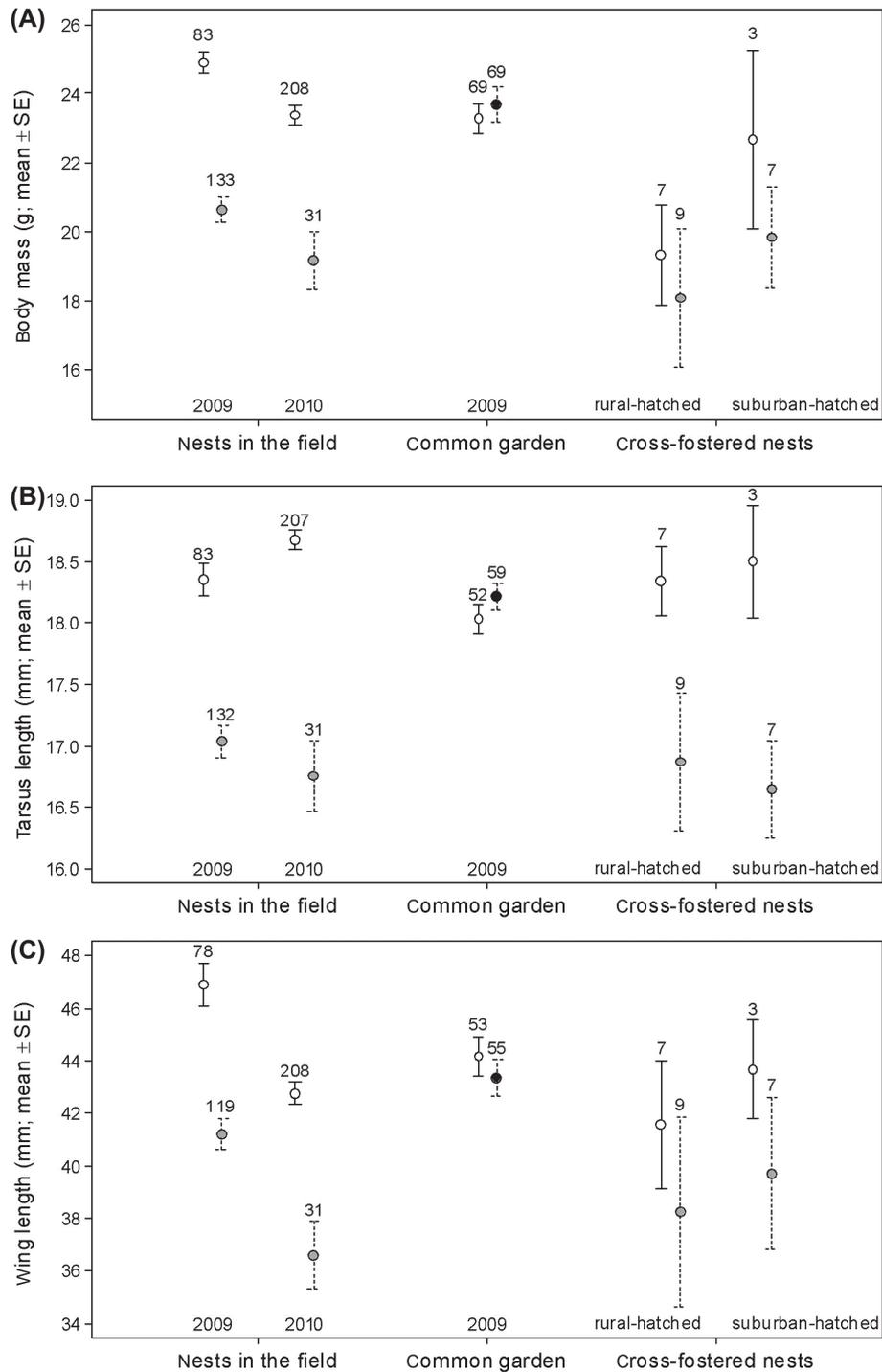
Figure 4. Nestling growth in rural (white) and suburban (grey) nests in the field, and in nests of rural (white) and urban (black) pairs in the common garden experiment. The number of nestlings is shown above each error bar.

by n = 2 pairs) as nestlings of rural pairs (19.56 ± 3.31 g, n = 16 nestlings by n = 5 pairs; LME: $t_5 = 0.45$, p = 0.674). In 2009, median clutch size was 4 eggs for both rural and urban pairs (Table 4); 18 out of 38 rural and 9 out of 30 urban nesting attempts failed to hatch nestlings. The apparently higher rate of unsuccessful nesting attempts in rural birds was mainly due to one pair who laid 7 clutches that all failed to hatch. Among the nests that hatched at least one nestling, hatching success was not different between rural and urban pairs (Table 4); median number of hatchlings was 3.5 for rural pairs and 3 for urban pairs. The median number of nestlings before fledging was 3 for both rural and urban pairs (Table 4, Fig. 3), thus they had similar fledging success (Table 4). Nestlings' body mass, tarsus length, and wing length did not differ significantly between rural and urban pairs (Table 4, Fig. 4). Among the 23 young that survived to adulthood (i.e. September), birds of urban and rural origin had similar body mass

Table 3. Number of visits with food items of various size by parents to field nests in 2010, and the percentage of nest observations during which the given visit type occurred at least once.

	Tiny[1]	Medium[2]	Large[3]	Unknown[4]
Suburban nests				
delivered by male	2	2	1	19
delivered by female	8	2	0	26
parents' summed deliveries	10	4	1	45
% of nest visits	16.7	6.7	1.7	75
% of food items	66.7	26.7	6.7	–
% of nest observations	40	40	10	70
Rural nests				
delivered by male	9	4	11	56
delivered by female	3	4	4	87
parents' summed deliveries	12	8	15	143
% of nest visits	6.7	4.5	8.4	80.3
% of food items	34.3	22.9	42.9	–
% of nest observations	42.3	23.1	46.2	92.3

[1]Smaller than the parent's bill (≤ 0.6 cm).
[2]Similar size as the parent's bill (ca 1 cm).
[3]Larger than the parent's bill (> 2 cm).
[4]We did not see the parent's bill clearly.

(27.02 ± 2.69 g vs 27.22 ± 2.25 g; LME: $t_8 = 0.54$, p = 0.605) in both years (habitat $\times$ year interaction: p = 0.164). Urban and rural parents fed their nestlings at similar frequency (Table 4).

Captive birds' brood size was similar to (Fig. 3) and nestling body mass was larger than (Fig. 4) those observed in the 'neighboring' free-living suburban sparrows in the same year ($t_{246} = 7.94$, $p < 0.001$). The proportion of hatched nestlings that survived until pre-fledging age per brood (0.94 ± 0.03) was also significantly higher than the survival rate we observed in suburban broods in the field (0.66 ± 0.05; $t_{85} = 4.09$, $p < 0.001$).

Cross-fostering experiment

Irrespective of their origin (i.e. hatching environment), nestlings in rural nests tended to grow larger than nestlings developing in suburban nests; this trend was most pronounced for tarsus length (Fig. 4). On the other hand, nestlings that hatched in different habitats but were raised in the same habitat showed less consistent tendencies in body size differences, i.e. rural-hatched nestlings had somewhat smaller body mass and wing length but similar or slightly longer tarsi than suburban-hatched nestlings when reared in the same environment (Fig. 4).

Discussion

Our study has provided four key results. First, the national monitoring data indicate a moderate decline in the Hungarian house sparrow population for the last decade, that is paralleled by the decreasing nest box occupancy and fledgling number in our suburban study site. Second, we found that the growth and survival of nestlings was reduced

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

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

[1]Intercept: 1.40 ± 0.06; n = 68 broods by 21 pairs.
[2]Intercept: -0.03 ± 0.18; n = 41 broods by 19 pairs.
[3]Intercept: 1.50 ± 0.27; n = 41 broods by 19 pairs.
[4]Intercept: -0.25 ± 0.09; n = 41 broods by 19 pairs.
[5]Intercept: 24.39 ± 0.64; n = 112 nestlings from 36 broods by 19 pairs.
[6]Intercept: 14.80 ± 1.65; n = 111 nestlings from 36 broods by 19 pairs.
[7]Intercept: 30.48 ± 1.82; n = 111 nestlings from 36 broods by 19 pairs.
[8]Intercept: 0.86 ± 0.55; n = 294 observations for 37 broods by 19 pairs.

in suburban nests, demonstrating that house sparrows may have similar difficulties with breeding in urbanized habitats in our moderately declining central-European population as in the rapidly declining British population. Third, our direct observations of parents' food deliveries revealed that suburban sparrows brought less 'e-prey' to their nestlings than rural parents, thus nestlings received less and/or lower quality food in more urbanized areas. Finally, we obtained two independent lines of experimental evidence that the rearing environment of nestlings plays a key role in the observed habitat differences in house sparrows' breeding success. We provide a detailed discussion of these results below.

The limited information that is available on the status of house sparrow populations in central European countries indicates a slight to moderate decline in this region (Kelcey and Rheinwald 2005, Reif et al. 2006). Our data on the Hungarian population revealed a similar trend, supporting the anecdotes we often hear about 'disappearing' sparrows. Further studies are in progress to test whether local population trends are related to the intensity of habitat urbanization in Hungary. Such studies will help to clarify the role that urbanization and its negative effects on breeding success play in the declines of the house sparrow.

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

Inadequate nestling diet is assumed to be a major cause for the low productivity and thereby the declines observed in urbanized sparrows (De Laet and Summers-Smith 2007, Peach et al. 2008, Shaw et al. 2008, Chamberlain et al. 2009). Our study provides direct evidence for the hypothesis that suburban nestlings receive diets of lower quality and/or quantity, as their parents delivered significantly fewer large prey items such as large caterpillars or beetles than those in rural habitats. Such 'e-prey' seems to be the most valuable type of nestling food since its delivery rate strongly predicts fledging mass and recruitment (Schwagmeyer and Mock 2008). In contrast, the frequency of parents' feeding visits was similar in suburban and rural broods. Thus, our finding likely reflects differential availability of large arthropods in differently urbanized habitats. It is not yet known whether 'e-prey' is superior merely due to the disproportionately larger quantity of nutrients it provides (Schwagmeyer and Mock 2008) or because it represents specific taxa of particular nutritional value (e.g. spiders contain high levels of taurine, Ramsay and Houston 2003). In either case, urbanization is likely to reduce diet quality for sparrow nestlings because they are primarily fed by beetles, caterpillars, flies, spiders and aphids (Anderson 2006). With the exception of aphids, these taxa tend to show reduced abundance and diversity with increasing urbanization (Shochat et al. 2004, McIntyre and Rango 2009, Niemelä and Kotze 2009, Raupp et al. 2010), whereas arthropods positively affected by urbanization are typically smaller sized (such as aphids) or unavailable for sparrows (e.g. gall-forming taxa; Raupp et al. 2010). Furthermore, the size of individual arthropods within taxa is also reduced in urbanized and polluted environments (Niemelä and Kotze 2009, Zvereva and Kozlov 2010), which may further decrease the availability of 'e-prey'. Peach et al. (2008) found that nestling survival was positively correlated with aphid abundance which might indicate that the lack of 'e-prey' could be (at least in part) compensated for by smaller prey that is available in urban environments. However, the authors suggested that their finding reflects a correlation between the abundance of aphids and other invertebrates rather than any dependence of sparrow nestlings on aphids.

The importance of nestling diet is further highlighted by our common garden experiment, which showed that urban and rural sparrows perform equally well in every aspect of reproduction if they live in the same environment with ample supplies of arthropod prey. Birds captured at urban sites showed no sign of reduced fertility or parental quality as an eventual consequence of their previous urban life. Thus, although adult sparrows from more urbanized habitats have smaller body mass (Liker et al. 2008, Bókony et al. 2010, 2012), their reproductive capacity does not seem to be inferior to that of rural sparrows. Furthermore, the captive birds' nestlings grew larger than those of the free-living suburban birds, reaching similar size as the chicks of the free-living rural birds (Fig. 3). Because the captive birds experienced the same weather conditions and pollution levels as the free-living suburban birds but had ad libitum access to nestling food, we might infer that the latter may be the most important determinant of breeding success for sparrows while weather and pollution seems to affect them via their effects on the availability of arthropods rather than directly.

The trends revealed by our cross-fostering experiment provide additional support for the importance of environmental

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

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

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

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