



Invertebrate prey availability limits reproductive success but not breeding population size in suburban House Sparrows *Passer domesticus*

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Factors affecting avian demography and abundance in urban landscapes are poorly understood and this hinders attempts to manage urban bird communities. Several recent studies indicate that lack of invertebrate prey in urban landscapes may constrain avian productivity and fitness relative to that in other habitats. House Sparrow *Passer domesticus* populations have undergone large declines in many European urban centres and inadequate reproductive success linked to invertebrate availability has been postulated as a potential cause of these declines. We conducted a replicated supplementary feeding experiment to test whether the availability of invertebrate prey limits the breeding success and adult abundance (colony size) of House Sparrows in suburban London, where House Sparrow populations declined by 60% during the decade preceding our study. Daily mealworm provision over two successive breeding seasons, sufficient to provide 82% of chick energy requirements of House Sparrow pairs nesting within 50 m of feeders, had a large positive impact on the abundance of recently fledged birds (+62%), but only a small positive impact, limited mainly to small colonies, on the overall abundance of territorial males. Colony growth was only weakly related to fledgling abundance in the previous year and did not appear to be constrained by nest-site availability. Conservation interventions that enhance invertebrate availability for suburban House Sparrows may increase reproductive success but are unlikely, on their own, to lead to population growth or recovery.

Keywords: mealworms, population dynamics, supplementary feeding, urban.

Environmental factors affecting avian demography and abundance in urban landscapes are poorly understood (Newton 1998, Shochat *et al.* 2006). Such knowledge is increasingly policy-relevant as interest in urban wildlife management grows and the proportion of humans living in urban centres continues to rise (United Nations 2008). Motivations for this growing interest include concern for biodiversity loss (Davies *et al.* 2011), a need to manage human–wildlife conflicts (e.g. Thomas *et al.* 2012) and growing evidence of the benefits to human well-being of exposure to greenspace and wildlife (Fuller *et al.* 2007, Barton & Pretty 2010). Avian reproductive success is generally lower in urban than in other landscapes, probably

mainly as a consequence of food limitation (Chamberlain *et al.* 2009), although predator impacts can be high (Bonnington *et al.* 2013). Most previous studies of factors affecting avian abundance and distribution have relied upon correlative approaches to identify patterns of association with measures of urbanization (Mennechez & Clergeau 2006), habitat extent or complexity (Mason 2006), potential competitors and predators (Sims *et al.* 2008, Thomas *et al.* 2012) and supplementary feeding (Fuller *et al.* 2008). These studies have often lacked mechanistic insights as a consequence of confounding correlation between environmental variables and a lack of experimental manipulation.

The House Sparrow *Passer domesticus* is ubiquitous in both agricultural and urban–suburban landscapes across most of its global range (Anderson

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2006). However, since the late 1970s, population declines have been reported from several continents including Europe (Shaw *et al.* 2008), North America (Erskine 2006) and Australia (Olsen *et al.* 2003), with major declines in agricultural and urban landscapes (Summers-Smith 2003, Shaw *et al.* 2008). Population changes are probably best documented in England, where overall abundance declined by 71% between 1971 and 2007, with declines on farmland occurring earlier, between the late 1970s and the mid-1990s (Robinson *et al.* 2005), than those in urban–suburban areas, which started 10 years later and were most rapid during the late 1990s and early 2000s (Summers-Smith 2003).

Environmental factors that might have contributed to declines in House Sparrow populations include reduced availability of seed and grain on farmland (Hole *et al.* 2002, but see von Post *et al.* 2013), predation by domestic cats *Felis catus* (Thomas *et al.* 2012) and Sparrowhawks *Accipiter nisus* (Bell *et al.* 2010) and loss of nesting sites (Summers-Smith 2003). House Sparrow chicks are reliant on a largely invertebrate diet, although independent young and adults are largely granivorous (Anderson 2006). Studies in England and Hungary have found relatively high rates of chick starvation and low fledgling body mass related to the local availability and quality of invertebrate prey (Peach *et al.* 2008, Seress *et al.* 2012). In particular, the provisioning of larger invertebrate prey, such as lepidopteran larvae and Orthoptera, to nestlings is associated with higher fledgling body mass, which in turn is positively related to the likelihood of recruitment as a breeding adult (Ringsby *et al.* 1998, Schwagmeyer & Mock 2008). These observations suggest that House Sparrow reproductive success, fledgling fitness and subsequent survival and recruitment are limited by the availability of larger invertebrate prey for nestlings, and the availability of such prey may be particularly limiting in urban–suburban environments. Extensive monitoring of reproductive success across Britain has highlighted a reduction in average brood size since the early 1990s (Baillie *et al.* 2014) consistent with a widespread increase in chick mortality that broadly coincided with the timing of the population decline in urban areas. Whole nest survival rates and the number of fledglings per nesting attempt have shown shallower declines since the early 1990s (Baillie *et al.* 2014) but these measures exclude partial brood mortal-

ity, which accounted for 44% (of 267 chicks dying from 232 broods) of total chick mortality in a declining suburban population (Peach *et al.* 2008).

We report the findings of a replicated supplementary feeding experiment to test the prediction that invertebrate availability limits reproductive success and population size in suburban House Sparrows. We predicted that invertebrate provision would increase reproductive success (Peach *et al.* 2008, Seress *et al.* 2012) and lead to local population growth as a consequence of enhanced fledgling survival and recruitment (Ringsby *et al.* 1998, Schwagmeyer & Mock 2008). A recent nest-box study confirmed the first of these predictions during a single breeding season, as mealworm provision enhanced clutch size, chick survival and fledgling production (Peach *et al.* 2014), but the study did not consider impacts on population growth. The present study was conducted at 66 sparrow colonies spread across Greater London, where House Sparrow abundance declined by 60% between 1994 and 2006 (Raven *et al.* 2007). This decline was widespread across the city, with negative trends in House Sparrow counts evident at 76 (statistically significant at 42) of 86 Breeding Birds Survey (BBS) 1-km squares surveyed over a period of at least 4 years between 1994 and 2004 (British Trust for Ornithology unpubl. data). Although supplementary feeding of birds in gardens is a worldwide phenomenon (Robb *et al.* 2008), this is the first experimental study we know of that has tested for impacts of food supplementation on population size for any vertebrate within an urban landscape. The House Sparrow is an ideal subject for experimental feeding studies because supplementary food is readily taken and the highly sedentary behaviour of this species (Fleischer *et al.* 1984, Anderson 2006), especially in urban environments (Heij & Moeliker 1990, Vangestel *et al.* 2011), reduces the likelihood of any confounding effects of dispersal. The study was intended to inform any conservation programmes that might aim to recover depleted urban House Sparrow populations.

METHODS

Study design

The study was conducted at 66 House Sparrow colonies spread across Greater London in localities dominated by private housing and domestic

gardens. Daily supplementary feeding of live mealworms (larvae of the beetle *Tenebrio molitor*) was established at 27 colonies during the breeding season (late April to early August) of 2005, with 27 unfed colonies serving as controls. The timing of mealworm provision was intended to coincide with the period when chicks were present in nests (the average hatch date over three breeding seasons in suburban Leicester was 2 May; data from Vincent 2006), and probably started too late to affect the timing or size of most first clutches. The same treatments were imposed at the same colonies in 2006, with an additional six fed and six unfed colonies (i.e. 33 colonies in each treatment category). The samples of fed and unfed colonies were similar with respect to geographical location, habitat character (including the extent of green space and housing density), initial colony size, background supplementary feeding by residents (mainly seed) and density of domestic cats (Peach *et al.* 2013). The distances between study colonies (mean and minimum nearest neighbour distances between fed and unfed colonies were 2.89 and 1.29 km, respectively) were large enough to ensure that provisioning adults from unfed colonies did not have access to our mealworms (Heij & Moeliker 1990, Bower 1999, Shaw 2009). Movements between colonies between years were probably also rare, as most House Sparrows breed within 1 km of their birth sites (Cheke 1972, Fleischer *et al.* 1984), with natal dispersal averaging only 0.21 km in Britain (Paradis *et al.* 1998), and 0.17 km (males) and 0.29 km (females) in Michigan, USA (Anderson 2006). Breeding dispersal averages 0.15 km in Britain (Paradis *et al.* 1998) and rarely exceeds 1–2 km (Summers-Smith 1988).

At each fed colony, live mealworms were provided twice each day (morning and late afternoon) at two or three feeding locations (all in residential gardens), each within 40 m (most were within 20 m) of an active House Sparrow nest. All mealworms were typically consumed within 30 min of provision and it was rare for any mealworms to be found in feeders at the next provisioning event. As mealworms were typically only available for < 1 h each day, chicks at most fed colonies were provisioned through the rest of the day with non-mealworm prey. The average daily provision of mealworms was 103 g at most colonies (*c.* 900 mealworms, 32% small and 68% large, providing 194 kcal of energy), but was 69 g (600 mealworms, 130 kcal) at five colonies in 2005 and at

two colonies in 2006. Surveys of feeder usage indicated that 96% of mealworms were taken by House Sparrows, 70% being taken by adults (60% carried away, 10% eaten) and 26% by juveniles or females (12% carried away, 14% eaten; Peach *et al.* 2013). Of the 60% of total mealworms carried away by adult Sparrows, 35% were carried by females and 25% by males. Adult House Sparrows typically carried away three to five mealworms at a time and, although we frequently observed adults feeding mealworms to chicks and fledglings away from feeders, and occasionally saw adults consume mealworms at feeders, we never saw adults consuming mealworms away from feeders. Our supplementary feeding therefore had the potential to influence directly the condition and survival of breeding adult Sparrows and fledged young, as well as reproductive success. Delayed impacts of our feeding on fitness or survival were also possible (Harrison *et al.* 2011).

Surveys of House Sparrow abundance

The abundance of territorial male Sparrows was assessed through two systematic surveys conducted between mid-March and mid-May at each colony during 2005, 2006 and 2007. Surveys were conducted between 06:00 and 11:00 h on dry, still (wind speed < 15 km/h) mornings and distinguished 'chirping' territorial males from non-chirping males and females (De Laet *et al.* 2011). Surveys covered a fixed core area that was centred on colony nesting sites and extended 50 m beyond the locations of all territorial males associated with the colony during the first survey year (mean core area = 1.7 ha, range 0.8–3.2 ha), plus a surrounding buffer area extending 200 m beyond the perimeter of the core area (mean of core plus buffer = 25.4 ha, 18.1–37.5 ha). Nest-sites within suburban House Sparrow colonies are typically located within a 25-m radius of a central point and are separated from neighbouring colonies by a distance of at least 50 m (Summers-Smith 1963, W. Peach pers. obs.). The intended function of the 50-m extension was to distinguish breeding pairs with ready access to our supplementary food (provided only within core areas) from those that would have to fly further to gather such food. Previous studies of provisioning behaviour in suburban House Sparrows have shown that most foraging occurs within 50 m of the nest ('mostly' within 50 m of the nest (Heij & Moeliker 1990),

71% within 70 m of the nest (Bower 1999), 95% within 50 m of the nest (Mitschke *et al.* 2000), 95% of movements within 16 m of the tagging location (Shaw 2009)). Surveys in the 200-m buffer allowed us to test for wider scale impacts of our supplementary feeding, and to assess any local re-distribution of territorial males in response to feeding. The size of this buffer zone was constrained by the available observer effort. During each survey, one of five trained observers walked a fixed survey route that followed all accessible rights of way plus a fixed set of private gardens. Maximum counts of chirping males in the core survey area (MCM_c) provided a year-specific measure of apparent breeding colony size, which when added to maximum counts in the 200-m buffer (MCM_b) provided a wider measure of local breeding population size (MCM_{cb}).

It was not possible to measure reproductive success directly, as nearly all nesting attempts were inaccessible, mostly in roof spaces. We therefore used age ratios (counts of fledgling Sparrows relative to MCM_c) as an indirect measure of reproductive success at the colony scale. During 2005 and 2006, three surveys of fledgling and juvenile Sparrows were conducted at approximately monthly intervals at each colony between mid-May and mid-August. These were conducted between 07:00 and 13:00 h and followed a fixed route within an area extending 50 m beyond the perimeter of the core survey area (mean size of these core areas plus 50-m buffers = 5.6 ha, range 3.3–8.1 ha) to allow the detection of any locally dispersing young. Trained observers slowly walked the fixed transect route and used a variety of calls and adult behavioural cues to locate and distinguish recently fledged Sparrows (fluffy plumage, yellow bill flange, weak flight, often concealed in woody vegetation and difficult to flush) from older juveniles (flat plumage, faded bill flange, strong flight, mobile often in flocks, readily flushed). The former are distinguishable from the latter for approximately 7–14 days after fledging (Summers-Smith 1963). Fledglings are fed by parents for 10–14 days after fledging, and are reliant on their parents for food during the first 7 days after fledging (Weaver 1942, Summers-Smith 1963). There is little quantitative information describing the dispersal of recently fledged House Sparrows, although all observations of fledged young between mid-April and mid-July at a suburban colony in Germany occurred within a 1.8-ha area

(equivalent radius *c.* 76 m) centred on the colony (Bower 1999).

Our measure of reproductive success for each colony in each year was the aggregate count of fledglings (summed across the three surveys) recorded within the core survey area divided by MCM_c . The aggregate fledgling count in the core area was highly correlated with the count in the core plus 50-m buffer ($r = 0.92$ in 2005, $n = 54$; $r = 0.93$ in 2006, $n = 66$). Summed fledgling counts from the three monthly surveys provided a similar measure of cross-colony variation in age ratio as did a more intensive sampling regime based on weekly counts (Peach *et al.* 2013). Fledgling counts in core survey areas were positively correlated with counts of Sparrow nests containing chicks (in the same areas) both across colony-years ($r = 0.72$, $n = 16$) and across surveys (see Peach *et al.* 2013 for details), suggesting that the former provide a useful measure of local variation in nesting success both between colonies and between surveys. Unlike fledglings, the detectability of juvenile House Sparrows may have been influenced by our feeding treatment (Peach *et al.* 2013), so juvenile counts are not considered here. We note, however, that the effect of mealworm provision on juvenile counts was qualitatively identical to that described here for fledglings.

Estimating the proportion of total chick energy requirements satisfied through mealworm provision

To aid interpretation of any effects of our feeding on House Sparrow abundance, we combined published information on chick energy requirements with data describing the seasonal pattern of nesting phenology for suburban House Sparrows to estimate the proportion of total chick energy requirements (over an entire breeding season) that was potentially satisfied by our mealworm provision. To do this we used an empirical model of nesting phenology and breeding success (from Peach *et al.* 2008) to predict the number of live chicks (in each of three age classes: 0–5 days, 5–10 days, 10–14 days) expected on each day of the breeding season. This model used observed reproductive parameters from suburban Leicester in 2002, where reproductive success was probably sufficient to maintain population size, and assumed no chick mortality, as nutritional stress was the main cause of chick mortality (Peach *et al.* 2008). For each

day of the breeding season we multiplied the predicted numbers of live chicks in each age class by the average daily energy requirement for chicks of that age class (from Blem 1975) to estimate the total energy required to sustain all chicks in the colony. This colony-scale energy requirement exhibited a pattern of seasonal variation similar to the proportion of Sparrow pairs with chicks (see Endnote B in Peach *et al.* 2013). We compared this daily chick energy requirement with our fixed daily provision of energy through mealworms. The latter was estimated using laboratory measures of the calorific content of our mealworms (mean \pm 1 se kcal derived from ten 100-g samples of both small and large mealworms = 166.6 ± 1.2 and 196.3 ± 1.6 , respectively; FA Labs, Stoke-on-Trent, UK), multiplied by a colony-specific estimate of the proportion of mealworms carried away by adult Sparrows during feeder usage surveys (Peach *et al.* 2013). Thus, for each day of the breeding season during each colony-year, we compared the predicted colony-wide chick energy requirement with the energy provided in mealworms carried away from feeders by adult Sparrows, and where the former exceeded the latter, we calculated by subtraction the daily energy shortfall. Summing the colony-wide energy requirement and any shortfall across the entire breeding season provided an estimate of the proportion of total chick energy requirements that was potentially satisfied by our mealworm provision. These calculations were repeated for each fed colony using both MCM_c and MCM_{cb} as estimates of the putative minimum and maximum numbers of Sparrow pairs that were feeding our mealworms to their chicks. Maximum counts of adult male House Sparrows at feeders suggested that some pairs nesting beyond core areas were taking mealworms from our feeders (Peach *et al.* 2013). To allow for the increasing component of non-invertebrate prey in the diets of older chicks, we repeated these calculations assuming that the proportion of the daily energy requirement that needed to be satisfied from invertebrate prey was equal to the proportion (by mass or volume) of invertebrates in the overall diet, with data for the latter coming from Anderson (2006). A lack of knowledge of chick protein requirements prevented us from estimating the extent to which our supplementary feeding covered protein needs. For reference, the average content of 100 g of mealworms (derived from the same laboratory analysis of the 20 meal-

worm samples described above) was 181.5 kcal energy, 19.1 g of protein, 5.9 g of carbohydrate, 9.1 g of fat and 64.5 g of moisture.

Nest-site availability

Nest-site availability was a factor that might conceivably have constrained increases in breeding population size. To assess the likelihood of any such constraint, we estimated the availability of unoccupied (by birds) potential nesting sites in a representative sample of properties (mean = 22 properties/colony) from 60 of the 66 core survey areas. Each property was scored according to its relative size (1–5) and accessibility to nesting Sparrows (yes = 1, no = 0). Accessibility was assessed using features such as missing or dislodged roof-tiles, gaps around soffit boards and the presence of creeping vegetation on walls.

Statistical analysis

Generalized linear mixed models (GLMMs) with Poisson error distributions were used to assess whether supplementary feeding influenced the abundance of fledgling and territorial male House Sparrows. Dependent variables were year- and colony-specific core counts of fledglings and the maximum counts of chirping males in core (MCM_c) and core plus buffer (MCM_{cb}) survey areas. The fledgling GLMM included the natural logarithm of year-specific MCM_c counts as an offset to convert raw fledgling counts to per-capita measures of fledgling abundance. Fixed factors included OBSERVER (three-level factor for fledglings, five-level factor for MCMs), YEAR (2005–2006 for fledglings; 2005–2007 for MCMs) and feeding treatment (FED or unfed colony). Because approximately the same quantity of mealworms was provided at each colony (irrespective of colony size), we assessed whether any numeric responses to supplementary feeding differed between three colony or local population size classes, defined using MCM counts during the first year of survey (colony $SIZE_c$: $MCM_c < 6$ = small, 6–8 = medium, > 8 = large; local population $SIZE_{cb}$: $MCM_{cb} < 16$ = small, 16–26 = medium and > 26 = large). Because there was evidence that adult House Sparrows nesting beyond core surveys took mealworms (Peach *et al.* 2013), we used $SIZE_{cb}$ in analyses of fledgling counts. We used $SIZE_c$ in analyses of MCM_c and $SIZE_{cb}$ in analyses

of MCM_{cb} . We tested all potential interactions between FED, YEAR and SIZE. COLONY was included as a random factor in all GLMMs to allow for the non-independence of counts from different years, and COLONY*YEAR was included in fledgling models to deal with over-dispersion (MCM counts were not overdispersed; $\chi^2/df < 1.7$). Given the timing of the introduction of mealworms (from late April 2005), any effect of feeding could have been immediate on fledgling counts but was unlikely to have influenced MCM counts until the calendar year after the introduction of feeding (age at first breeding is 1 year for most House Sparrows; Anderson 2006). Thus, any effect of feeding on MCM counts should have been evident in interactions involving FED and YEAR. We checked whether any impact of our feeding on House Sparrow abundance was dependent on the estimated consumption of mealworms but found no evidence that it was (Supporting Information Appendix S1, Tables S1 and S2), thus supporting the use of a simple fed–unfed comparison.

Two additional ‘nuisance’ variables were included in the GLMM of fledgling abundance. First, the proportion of MCM_{cb} counts in the 200-m buffer (MCM_b/MCM_{cb} or ‘PBUFF’) provided a colony-year-specific measure of the likelihood of fledglings originating from nests in the 200-m buffer subsequently being recorded in the core area as a consequence of immigration. Given the limited mobility of fledglings (weak fliers, difficult to flush) it seems unlikely that fledglings from nests beyond 200-m buffers could have dispersed as far as core survey areas. Previous analyses (based on 4 years of fledgling counts) indicated the strength of the PBUFF effect did not differ between fed and unfed colonies (Peach *et al.* 2013), and we repeat and extend those analyses for the 2 years of fledgling counts considered here. Specifically, we assess whether the magnitude of any effect of mealworm provision on fledgling counts differed between colony-years with contrasting likelihoods of fledgling immigration. We did this by testing for an interaction between FED status and PBUFF (see Results) and by comparing the magnitude of the effect of mealworm provision on fledgling counts for groups of colony-years with contrasting PBUFF scores (Supporting Information Appendix S2, Tables S3 and S4). Secondly, as our suburban study areas were dominated by residential properties with gardens, access to potentially suitable Sparrow habitat was incomplete and differed

between colonies. We therefore tested whether the proportion of potentially suitable habitat that was accessible to observers (ACCESS) influenced fledgling counts (MCM counts were probably less sensitive to restricted access as territorial males usually call from conspicuous vantage points where they were readily detected without access to individual gardens). Neither PBUFF nor ACCESS differed between fed and unfed colonies (mean \pm se PBUFF: 0.63 ± 0.02 vs. 0.62 ± 0.02 respectively, $t_{252} = 0.7$, $P = 0.47$; ACCESS: 0.45 ± 0.03 vs. 0.51 ± 0.03 respectively, $t_{64} = 1.3$, $P = 0.2$).

Finally, we tested whether between-year changes in MCM counts (at the core and core plus 200-m buffer scales) were related to per-capita fledgling abundance. To do this we fitted a GLMM with Poisson errors in which MCM count in the second year was the dependent variable, the logarithm of MCM in the first year was an offset variable and COLONY was a random factor. Fixed effects were YEAR and the aggregate count of fledglings divided by MCM_c in the first year (square-root-transformed to correct a positive skew), plus an interaction between the two; the year and interaction terms were always non-significant ($P > 0.3$), so were removed from the model. We checked whether the fledgling effect was non-linear by including a quadratic fledgling term. Raw fledgling and MCM counts were corrected for any significant observer effects prior to analysis.

All GLMMs were fitted using procedures GLIMMIX and MIXED of SAS version 9.2 (SAS Institute, Cary, NC, USA), incorporating the Satterthwaite approximation for estimating degrees of freedom and Wald tests for the significance of fixed effects.

RESULTS

Proportion of chick energy requirements potentially satisfied by supplementary feeding

We estimate that our supplementary feeding should have been sufficient to satisfy 82% of total chick energy requirements of House Sparrows nesting within core survey areas (Table 1). The proportion of chick energy requirements provided for Sparrows nesting within core plus 200-m buffers varied between 58% for small colonies and 29% for large colonies, and averaged 37% across all colonies

Table 1. Proportion of predicted total chick energy requirements (kcal, summed across colony-years) potentially satisfied by our supplementary mealworm provision. Energy provision is considered at two spatial scales (core colony areas and core-plus-200-m buffers). Colony size categories differ slightly between core and core-plus-200-m buffer calculations. See 'Methods' for details of calculations.

| Scale/energy measures | Colony size | | | |
|-----------------------------------|-------------|---------|-----------|-----------|
| | Small | Medium | Large | All |
| Core | | | | |
| Number of colony-years | 24 | 18 | 18 | 60 |
| Total energy required (kcal) | 193 687 | 243 548 | 379 703 | 816 938 |
| Energy provision shortfall (kcal) | 16 072 | 34 600 | 92 662 | 143 334 |
| % requirement satisfied | 91.7 | 85.8 | 75.6 | 82.5 |
| Core + 200-m buffer | | | | |
| Number of colony-years | 21 | 19 | 20 | 60 |
| Total energy required (kcal) | 412 305 | 730 638 | 1 430 594 | 2 573 537 |
| Energy provision shortfall (kcal) | 171 479 | 429 919 | 1 010 322 | 1 611 720 |
| % requirement satisfied | 58.4 | 41.2 | 29.4 | 37.4 |

(Table 1). Considering the proportion of chick energy requirements expected to be provided by invertebrate prey, our mealworm provision could have satisfied 96% of predicted requirements of House Sparrows nesting in core areas and 55% of those nesting in core plus 200-m buffers (Supporting Information Table S5). The scale of our supplementary feeding was therefore sufficient to have had a substantial impact on House Sparrow breeding success at both the core and the core-plus-200-m buffer scales and across all colony sizes.

Effects of mealworm provision on fledgling abundance

After dropping the non-significant ACCESS term ($P > 0.5$) from the GLMM and allowing for observer and PBUFF effects, mealworm provision had a significant positive influence on per-capita fledgling counts (FED: $F_{1,49} = 9.4$, $P < 0.004$; Table 2). This effect of mealworm provision on fledgling counts did not vary with colony size (SIZE*FED: $F_{2,49} = 0.05$, $P = 0.95$) or between years (YEAR*FED: $F_{1,48} < 0.01$, $P = 0.95$), or in relation to PBUFF (footnote b, Table 2; Appendix S2, Table S4). The consistency of the effect of mealworm provision across a 10-fold variation in average PBUFF (Supporting Information Appendix S2 and Fig. S1) suggests a relatively minor influence of fledgling immigration on fledgling counts. Mealworm provision increased per-capita fledgling counts by an average of 62% (predicted means (95% confidence intervals) of 2.05 (1.65–2.55) vs. 1.26 (1.01–1.59)).

Table 2. Predictors of per-capita fledgling abundance at the core colony scale. Aggregate annual fledgling count in core survey areas was the dependent variable in a GLMM with a Poisson error structure and (\log_e) maximum counts of territorial males (MCM_c) as an offset term. Random terms were colony and colony*year. Fixed effects were observer, proportion of MCM in the 200-m buffer (PBUFF), year, colony size (small, medium, large: SIZE_{cb}) and feeding treatment (FED, unfed). P -values of each model term are listed, along with the direction of key significant terms. The model fitted the data well ($\chi^2/df = 1.10$).

| Model terms | P -value | Direction |
|----------------------------|------------|-------------|
| OBSERVER | 0.076 | |
| PBUFF ^{a,b} | 0.006 | Positive |
| YEAR | 0.070 | |
| SIZE | 0.341 | |
| FED | 0.004 | Fed > Unfed |
| YEAR*SIZE | 0.836 | |
| YEAR*FED | 0.950 | |
| SIZE*FED | 0.952 | |
| YEAR*SIZE*FED ^c | 0.204 | |

^aRemoving PBUFF from the model had little effect on the significance or parameter estimates of other model terms. ^bThe PBUFF effect did not differ between fed and unfed colonies (adding PBUFF \times FED to the above model: $F_{1,73} = 0.78$, $P = 0.38$). ^cRemoving the three-way interaction had little effect on the significance or parameter estimates of other model terms.

Effects of mealworm provision on the abundance of territorial males

After allowing for effects of observer, colony size and colony size*year, there was only weak evidence of any influence of mealworm provision on MCM counts (YEAR*SIZE*FED: $F_{4,166} = 2.3$,

Table 3. Predictors of maximum chirping male (MCM) counts at the core and core-plus-200-m buffer scales. Colony- and year-specific MCM counts are the dependent variables in GLMMs with a Poisson error structure, and colony declared as a random term. Predictive terms are observer, year, colony size (small, medium, large; SIZE_c for core, SIZE_{cb} for core + buffer) and feeding treatment (FED, unfed). *P*-values of each model term are listed, along with the direction of key significant terms. Both models showed adequate fit to the data ($\chi^2/df = 0.98$ and 1.64, respectively).

| Model terms | Core | | Core + 200-m buffer | |
|-------------------|-----------------|-----------|---------------------|-----------|
| | <i>P</i> -value | Direction | <i>P</i> -value | Direction |
| OBSERVER | 0.854 | | < 0.001 | |
| YEAR | 0.411 | | 0.208 | |
| SIZE | < 0.001 | Positive | < 0.001 | Positive |
| FED | 0.612 | | 0.266 | |
| YEAR × SIZE | 0.015 | Fig. S2 | 0.051 | Fig. 1 |
| YEAR × FED | 0.691 | | 0.445 | |
| SIZE × FED | 0.569 | | 0.287 | |
| YEAR × SIZE × FED | 0.064 | Fig. S2 | 0.066 | Fig. 1 |

$P = 0.064$ in core areas; $F_{4,166} = 2.3$, $P = 0.066$ in core-plus-200-m buffers; Table 3). Mealworm provision had no impact on MCM counts at large and medium-sized colonies but had a positive impact on MCM counts at small colonies, which was evident in 2006 and 2007 at the core-plus-200-m buffer scale (Fig. 1), and only in 2007 at the core scale (Supporting Information Fig. S2). Changes in core (MCM_c) counts at small fed colonies were uncorrelated with changes in buffer (MCM_b) counts during 2005–2006 ($r_9 = 0.17$, $P = 0.61$) and 2006–2007 ($r_{11} = 0.20$, $P = 0.50$), consistent with no re-distribution of territorial males between the two areas.

Considering the effect of feeding across all colonies irrespective of their initial size (i.e. dropping the YEAR*SIZE*FED term from the GLMMs in Table 3), indicated no overall effect of mealworm provision on MCM counts (YEAR*FED: $F_{2,170} = 0.05$, $P = 0.95$ in core areas; $F_{2,170} = 0.09$, $P = 0.91$ in core-plus-200-m buffers), the aggregate net gains in territorial males at small fed colonies (*c.* 57 individuals at the core-plus-200-m scale) being largely offset by net losses at medium-sized fed colonies (*c.* 37 individuals; Table 4). Across all 33 fed colonies, there was an overall net gain of approximately 34 territorial males between 2005 and 2007 (MCM_{cb} counts fell by 79 and 113

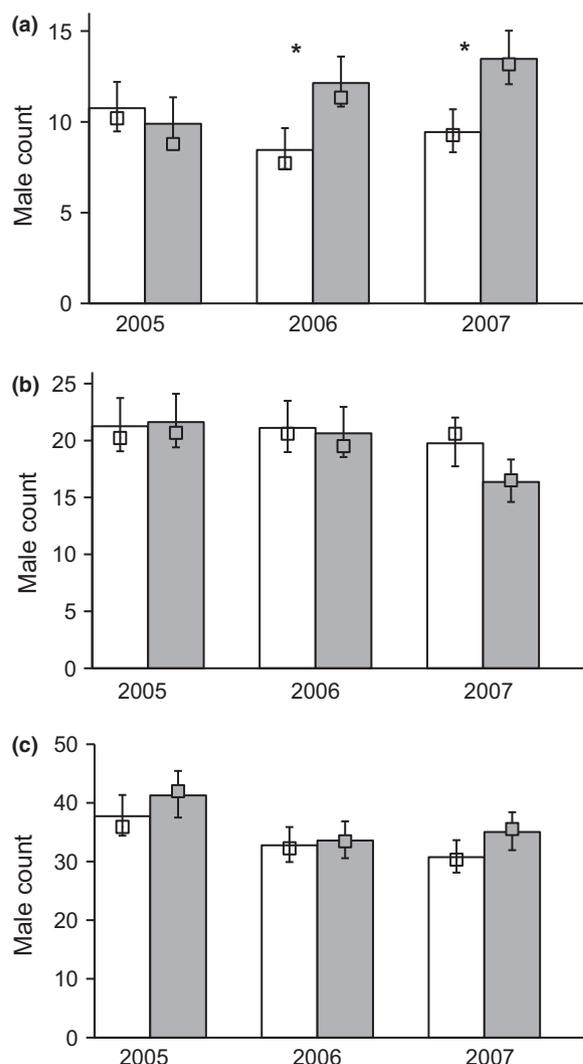


Figure 1. Mean maximum counts of territorial male House Sparrows within core-plus-200-m buffer areas during 2005–2007, classified as (a) small, (b) medium and (c) large colonies (see ‘Methods’ for details). Bars show predicted means (\pm se) and square symbols show raw means. Filled bars/symbols show fed colonies and open bars/symbols show unfed colonies. * Statistically significant (at $P < 0.05$) *post-hoc* differences between predicted mean counts at fed and unfed colonies for any colony size in any year.

at fed and unfed colonies, respectively, the difference being equivalent to 4.4% of 2005 counts; Table 4). Independent of any effect of feeding, there was a tendency for MCM counts to decline at medium and large colonies, and to remain stable at small colonies (YEAR*SIZE: $F_{4,166} = 3.2$, $P < 0.02$ in core areas; $F_{4,166} = 2.4$, $P < 0.06$ in core-plus-200-m buffers; Figs 1 and S2).

Table 4. Changes in predicted aggregate counts of territorial male House Sparrows (at the core-plus-200-m scale) on study colonies between 2005 and 2007 derived from the GLMM summarized in Table 3. Colony sizes are small (S), medium (M) and large (L).

| Fed status | Colony size (no. of colonies) | Year | | | Change between 2005 and 2007 | |
|------------|-------------------------------|-------|-------|-------|------------------------------|-------|
| | | 2005 | 2006 | 2007 | Absolute | % |
| Unfed | S (11) | 118.3 | 93.0 | 103.8 | -14.5 | -12.2 |
| | M (10) | 212.6 | 211.1 | 197.5 | -15.1 | -7.1 |
| | L (12) | 452.6 | 393.2 | 369.1 | -83.5 | -18.5 |
| | All (33) | 783.5 | 697.2 | 670.4 | -113.1 | -14.4 |
| Fed | S (12) | 118.6 | 145.7 | 161.6 | +42.8 | +36.0 |
| | M (10) | 216.2 | 206.3 | 163.5 | -52.6 | -24.3 |
| | L (11) | 454.1 | 369.2 | 385.3 | -68.8 | -15.2 |
| | All (33) | 789.1 | 721.1 | 710.4 | -78.6 | -10.0 |

Relationship between changes in the abundance of territorial males and per-capita fledgling abundance

Between-year changes in MCM counts (at both measurement scales) were positively related to per-capita fledgling abundance in core survey areas in the previous year (quadratic fledgling terms for (i) change in MCM_c ($F_{1,96} = 23.3$, $P < 0.001$, Fig. 2) and (ii) change in MCM_{cb} ($F_{1,102} = 4.7$, $P < 0.04$)). However, the relationship was weak at

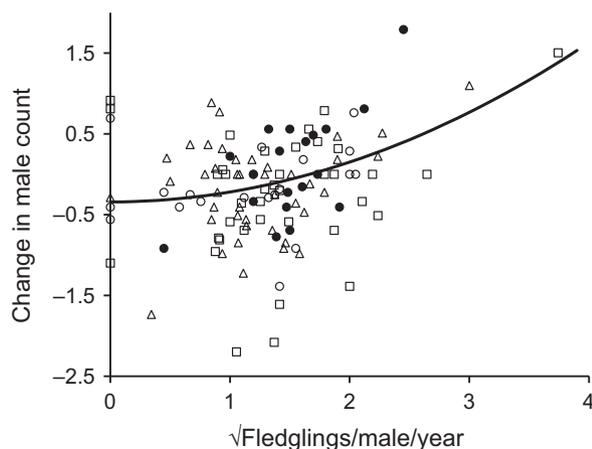


Figure 2. Relationship between changes in the counts of territorial male sparrows in core survey areas ($\log_e(MCM_{n+1}/MCM_n)$ where $n = \text{year}$) and per-capita fledgling counts (aggregate annual count of fledglings/ MCM_n). Symbols represent colony size (circle = small, square = medium, triangle = large) and filled circles represent small, fed colonies (where changes in male counts were more positive; Fig. S2). The line shows the relationship predicted by the GLMM.

both scales (crude $r^2 = 0.07$ and 0.02 , respectively), suggesting that other demographic components were more important drivers of change in the abundance of territorial males.

Nest-site availability

The proportion of apparently accessible buildings averaged 50.2% and did not differ between colony sizes (ANOVA, Wald test: $\chi^2_2 = 1.65$, $P = 0.44$), fed status ($\chi^2_1 = 0.76$, $P = 0.38$) or the interaction between the two ($\chi^2_4 = 0.92$, $P = 0.63$). These results suggest that the abundance of territorial males was probably not constrained by nest-site availability.

DISCUSSION

The enhanced abundance of fledglings in core survey areas at fed colonies could at least partly have been a consequence of feeding-related fledgling immigration from surrounding areas rather than enhanced reproductive success within core areas. However, the consistency of the magnitude of the effect of mealworm provision on fledgling abundance across a 10-fold variation in the propensity for fledgling immigration (Appendix S2, Fig. S1) suggests that any such immigration effect was small relative to the likely impact of mealworm provision on House Sparrow reproductive success (Peach *et al.* 2014) and associated fledgling abundance. Thus, although the average increase in per-capita fledgling abundance (62%) may overstate the actual impact of our mealworm provision on House Sparrow reproductive success, it was similar in magnitude to the impact of mealworm provision on nesting success in suburban Leicester (55% more fledglings per nesting attempt; Peach *et al.* 2014). This study therefore provides experimental confirmation that invertebrate availability limits House Sparrow reproductive success in suburban landscapes, and our first prediction is upheld.

Maximum counts of adult male Sparrows at mealworm feeders suggested regular usage of feeders by pairs nesting beyond core areas (Peach *et al.* 2013). However, the same feeder counts (which over 1-min periods averaged 82% of MCM_c but only 24% of MCM_{cb}) and observations at identical feeders deployed in suburban Leicester (where 97% of mealworms were taken by Sparrows nesting within 26 m of feeders and the maximum distance at which provisioning adults collected

mealworms for chicks was 165 m; Peach *et al.* 2014) suggest that the intensity of usage of mealworm feeders in London is likely to have declined strongly with distance of nests from feeders and therefore to have been much lower for pairs nesting in 200-m surrounding buffers than for pairs nesting within core areas. Moreover, our mealworm provision was sufficient to cover most of the chick energy requirements of Sparrow pairs nesting within core areas and more than one-third of the chick energy requirements of all pairs nesting within core-plus-200-m buffers (Table 1). This high level of supplementary provision may explain why the magnitude of the impact of mealworm feeding on fledgling abundance was consistent across colony sizes, implying that competition for mealworms among Sparrows was not strong enough to influence colony-level reproductive success.

Previous studies have highlighted higher rates of chick starvation and reduced fledgling body mass for House Sparrows in urban landscapes possibly linked to a lack of large-bodied invertebrate prey such as caterpillars and beetles (Vincent 2006, Peach *et al.* 2008, Seress *et al.* 2012). Urbanization reduces the abundance and diversity of key invertebrate prey including beetles, caterpillars, Diptera and spiders (Shochat *et al.* 2004, Niemela & Kotze 2009, Vergnes *et al.* 2014). A lack of larger invertebrate prey may force (sub)urban House Sparrows to feed their chicks more smaller invertebrate prey (such as aphids) and vegetable material, which is associated with higher rates of chick mortality (Peach *et al.* 2008, Seress *et al.* 2012).

Despite covering a potentially high proportion of chick energy requirements and substantially raising reproductive success across all colony sizes, our supplementary feeding had little subsequent impact on the abundance of territorial male House Sparrows (Tables 3 and 4). This implies that the higher reproductive success failed to translate into enhanced local recruitment. Given the low rates of natal dispersal in this species, especially for males (e.g. in one USA study, 73% of male local recruitment, within 4.7 km of nests, was at the natal colony, Fleischer *et al.* 1984; average natal dispersal distance in Britain is just 0.21 km, Paradis *et al.* 1998), and the widespread House Sparrow population decline that occurred across Greater London between 1994 and 2006 (see Introduction), it is likely that any feeding-related enhancement in local recruitment would have been evident within

our core-plus-200-m survey areas. Our second prediction is therefore rejected: local population growth was generally insensitive to enhanced breeding season invertebrate availability and enhanced reproductive success. More generally, local population growth was only weakly related to our measure of reproductive success (Fig. 2). This implies that some other environmental factor (s), probably acting on demographic components other than reproductive success, was limiting local population size in London's suburban House Sparrows. Candidate limiting factors are poorly understood but might include habitat characteristics associated with the socio-economic status of residential areas and/or predation pressure (Shaw *et al.* 2008, Bell *et al.* 2010, Thomas *et al.* 2012).

Our finding that feeding-related increases in MCM counts were restricted to small colonies (Fig. 1) cannot be explained by higher per-capita fledgling counts at small fed colonies (as the effect of feeding on fledgling abundance did not depend on colony size). We cannot rule out the possibility that the increase in MCM counts at small fed colonies might have been caused by feeding-related immigration of territorial males from beyond the 200-m buffer, perhaps facilitated by the relatively low densities of territorial Sparrows in the core-plus-200-m buffers (0.38 territorial males/ha in small fed colonies in 2005, compared with 0.91 in medium, and 1.84 in large, fed colonies). It is also possible that colony growth at medium and large fed colonies was constrained by one or more environmental factors acting in a density-dependent manner to limit the survival or recruitment of the increased numbers of fledged young. For example, it is conceivable that the availability of nest-sites or winter food limited the growth of larger but not smaller colonies. However, our data describing nest-site availability suggest this factor probably did not limit the abundance of breeding Sparrows in any colony size category. The potential role of non-invertebrate food availability (primarily seed and other vegetable materials) in limiting survival and population size in suburban House Sparrows merits further investigation. Although it is possible our supplementary provision of mealworms could have had carry-over impacts on demographic rates after the period of feeding (Harrison *et al.* 2011), any such impacts were evidently too small to influence local breeding population size at most fed colonies.

Many previous studies have shown that avian reproductive success can be increased through the

provision of supplementary invertebrates or protein/energy-rich food (Newton 1998, Ruffino *et al.* 2014), although some studies show no (e.g. Bromssen & Jansson 1980) or even negative (Harrison *et al.* 2010) impacts of feeding during the breeding season. We know of only two previous studies conducted in urban landscapes, both showing positive effects of feeding on reproduction (Dhindsa & Boag 1990, Peach *et al.* 2014). Many studies have considered the effects of winter feeding on avian breeding densities (e.g. see table 7.10 of Newton 1998) but fewer have considered the impacts of manipulating breeding season food availability on subsequent population size. Breeding season food provision failed to influence the densities of breeding corvids (Yom-Tov 1974, Dhindsa & Boag 1990), and caterpillar removal achieved through insecticide application did not affect the densities of forest passerines (Cooper *et al.* 1990). However, management that increases food abundance for game bird chicks has been shown to enhance subsequent breeding densities (e.g. Watson & O'Hare 1979, Rands 1985).

In conclusion, this study demonstrated that invertebrate availability limits the reproductive success but not the abundance of breeding adult House Sparrows in suburban London. The factors that determine population size are poorly understood, but probably do not include nest-site availability. Conservation measures that enhance the abundance of invertebrate prey may increase the reproductive success of suburban House Sparrows, but are unlikely on their own to lead to population recovery.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Testing for an influence of mealworm intake on changes in House Sparrow abundance.

Appendix S2. Does the effect of feeding on fledgling abundance depend on the relative abundance of territorial males in areas surrounding core colonies?

Figure S1. Effects of mealworm provision (open bars = unfed, shaded bars = fed) and PBUFF category (low–intermediate–high) on per-capita fledgling counts.

Figure S2. Mean maximum counts of territorial male House Sparrows within core survey areas during 2005–2007, classified as (a) small, (b) med-

ium and (c) large colonies (see Methods for details).

Table S1. Predictors of per-capita fledgling abundance (including high–low mealworm provision) at the core colony scale.

Table S2. Predictors of maximum chirping male (MCM) counts (including high–low mealworm consumption) at the core and core-plus-200-m buffer scales.

Table S3. Characteristics of PBUFF categories (n = number of colony-years) including median (and range) PBUFF scores, and maximum chirping male counts in core (MCM_c) and surrounding 200-m buffers (MCM_b).

Table S4. Predictors of per-capita fledgling abundance (including high–intermediate–low PBUFF) at the core colony scale.

Table S5. Proportion of chick energy requirements predicted to be provided by invertebrate prey (kcal, summed across colony-years) potentially satisfied by our supplementary mealworm provision.