Urban Ecosystems (2018) 21:1053–1065
https://doi.org/10.1007/s11252-018-0784-4

Depleted suburban house sparrow *Passer domesticus* population not limited by food availability

Will J. Peach[1] · **John W. Mallord**[1] · **Nancy Ockendon**[1] · **Chris J. Orsman**[1] · **William G. Haines**[1]

Abstract

Little is known about the environmental factors that limit the demography and abundance of wild vertebrates in highly modified urban environments. The House Sparrow *Passer domesticus* is a globally widespread species whose urban populations have recently undergone substantial declines particularly in Europe. The environmental drivers of these declines remain unknown. In a previous study we showed that invertebrate availability during the breeding season limited reproductive success but not population size in a suburban sparrow population. In this study we test experimentally whether year-round food availability limits demography and population size. Supplementary feeding involved the provision of invertebrate prey (during the breeding season) plus unlimited high-energy seed (year-round) at 33 sparrow colonies spread across suburban London over two successive calendar years. Thirty-three unfed colonies served as controls. Supplementary feeding increased fledgling abundance, but had no impact on overwinter survival or population size. We conclude that this depleted suburban sparrow population is not limited by food availability, and conservation efforts based primarily on food provision are unlikely to succeed. We also tested whether cross-colony variation in sparrow abundance was correlated with a set of potential environmental stressors including measures of predator abundance and pollution. Sparrows were more abundant, or showed more positive temporal changes in abundance, at localities containing large areas of seed-rich habitat and low levels of nitrogen dioxide air pollution. Further research is merited into the potential impacts of air pollution on the fitness of urban birds.

Keywords Air pollution · Avian conservation · Avian demography · Food limitation · Supplementary feeding · Urban birds

Introduction

Urban landscapes provide biodiversity with a set of highly modified environmental conditions (Chase and Walsh 2006; Pickett et al. 2011). Compared to less modified landscapes, habitats are often fragmented and degraded, land, water and air are polluted by chemicals, noise and light, resource availability is modified, and predator abundance can be high (Shochat et al. 2006; Grimm et al. 2008). These conditions often negatively affect species richness and diversity (Clergeau et al. 2006; McKinney 2008), and evidence is accumulating of impacts of specific environmental factors on wild animals. For example, chemical pollution in the form of heavy metals or nitrogen oxides is known to cause oxidative stress (Kelly 2003; Koivula and Eeva 2010), anthropogenic noise affects foraging behaviour and reduces reproductive success (Barber et al. 2009; Schroeder et al. 2012) and artificial light affects circadian rhythms and spatial orientation (Gaston et al. 2013). Urban landscapes often support elevated densities of predators which can have a range of direct and indirect effects on prey fitness (Thomas et al. 2012; Bonnington et al. 2013). Some infectious diseases are more prevalent in urban landscapes sometimes linked to the spread of host species and sometimes exacerbated by human activities like supplementary feeding (Bradley and Altizer 2007; Robinson et al. 2010). Widespread supplementary feeding especially of birds in residential areas has a range of positive and negative impacts (Jones and Reynolds 2008; Hanmer et al. 2017). Invertebrate prey is often lacking in availability or quality in urban landscapes with potential fitness consequences for consumers of those prey (Isaksson and Anderson 2007; Chamberlain et al. 2009).

The House Sparrow *Passer domesticus* is a globally widespread urban-adapted species (Anderson 2006). In recent

---

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s11252-018-0784-4) contains supplementary material, which is available to authorized users.

✉ Will J. Peach
will.peach@rspb.org.uk

[1] RSPB Centre for Conservation Science, RSPB, The Lodge, Sandy, Bedfordshire SG19 2DL, UK

decades, evidence has emerged of substantial House Sparrow population declines in urban centres across Europe, Canada and India (Summers-Smith 2003; Erskine 2006; Shaw et al. 2008; Dandapat et al. 2010; Murgui and Macias 2010). For example, House Sparrow numbers declined by 60% across London during 1994–2006, and by 50% in the towns and cities of Lombardy, northern Italy during 1996–2006 (Raven et al. 2007; Brichetti et al. 2008). Environmental causes of these declines remain obscure but a variety of candidate drivers have been proposed. These include increased depredation associated with Sparrowhawks *Accipiter nisus* or domestic cats (Bell et al. 2010; Thomas et al. 2012), effects of air pollutants or electromagnetic radiation from telephone masts (Everaert and Bauwens 2007; Summers-Smith 2007), and nutritional constraints during reproduction (Peach et al. 2008; Seress et al. 2012). Invertebrates dominate the diets of House Sparrow chicks (Anderson 2006), and nestlings fed larger prey items tend to weigh more at fledging and are more likely to survive to recruit as breeding adults (Ringsby et al. 1998; Schwagmeyer and Mock 2008). A shortage of suitable invertebrate prey in urban-suburban environments could therefore affect nesting success, fledgling quality and survival during the first year of life. Lack of seed food on farmland has been shown to reduce the overwinter survival of House Sparrows (Hole et al. 2002) but there is little information on the likelihood of seasonal seed shortages in urban landscapes. There is however evidence of widespread losses of green and brown space, of trees and the conversion of residential gardens for housing or parking (e.g. London Assembly 2005, 2007; Pauleit et al. 2005), which is likely to have reduced the availability of important sparrow foraging habitats such as deciduous woody vegetation and grassland (Vincent 2006). It has been suggested that such habitat changes have been concentrated into more affluent urban districts which might account for the apparent persistence of House Sparrows in more socially deprived areas (Shaw et al. 2008).

In this study we tested experimentally whether food availability limits the demography and population size of a depleted suburban House Sparrow population. We previously reported that supplementary provision of invertebrate prey during the breeding season raised nesting success and fledgling abundance but had little impact on population size (Peach et al. 2015). The current study tested whether year-round food provision (incorporating breeding season invertebrates plus year-round high-energy seed) affected reproductive success, overwinter survival and population growth. The experiment was conducted across 66 House Sparrow colonies of widely contrasting environmental character. This variation allowed us to test whether colony-level demography, density and growth were related to a range of potential urban stressors such as predator density and pollution. The aim of the study was to test empirically whether food availability or other potential urban stressors constitute plausible drivers of House Sparrow population change in urban landscapes. The study is intended to inform future conservation programmes aimed at urban sparrow populations.

Despite the global extent of anthropogenic supplementary feeding of birds (Robb et al. 2008), our study appears to be the first experimental assessment of the demographic impact of seed provision in an urban environment, most previous studies having been conducted in rural landscapes where food supply is easier to manipulate (e.g. Brittingham and Temple 1988; Plummer et al. 2013). House Sparrows are particularly suited to such a study because they readily consume supplementary food and remain relatively sedentary throughout their annual cycle (Fleischer et al. 1984; Heij and Moeliker 1990; Anderson 2006; Vangestel et al. 2011).

Methods

Supplementary feeding

Supplementary feeding was conducted over four years at 66 House Sparrow colonies located across suburban Greater London in localities dominated by residential housing, domestic gardens and communal green space. During the first phase of the study (2005–06) supplementary feeding was restricted to daily provision of mealworms (live *Tenebrio molitor* larvae) throughout the sparrow breeding season. At each of 33 fed colonies, a fixed weight of mealworms (averaging 103 g per colony) was provided daily at 2–3 feeding locations per colony between late April and early August (starting in 2005 at 27 colonies, and in 2006 at a further 6). Thirty-three unfed colonies (matched against the sample of fed colonies for geographic location, sparrow abundance, habitat character, domestic cat *Felis catus* density and background supplementary feeding) served as controls (see Peach et al. (2013) for further details and site map). During a second phase of study, mealworm provision remained unchanged and was supplemented (from late May 2007 until March 2009) by ad libitum year-round provision of sunflower *Helianthus annuus* hearts. This energy-rich food was provided in plastic seed feeders at the same 2–3 locations per colony (usually domestic gardens) where volunteers maintained a continual supply of seed on every day of the year. It was common for birds to remove all mealworms from feeders within an hour of initial provision and although sunflower hearts were sometimes exhausted at individual feeders, the deployment of multiple feeders at each colony ensured experimental seed provision was maintained at all times. Provision of breeding season invertebrates plus unlimited year-round seed is expected to have satisfied the major dietary requirements of House Sparrows throughout the year (Anderson 2006) but is unlikely to have met all micro-nutrient or natural foraging requirements.

Total provision of sunflower hearts over the 23 months of phase two averaged 228.3 kg per colony (range 114.8–1032.8 kg). House Sparrows were by far the most frequent consumers of our supplementary food accounting for 96% of all mealworms (Peach et al. 2013) and were recorded consuming sunflower hearts during 78% of 2885 15-min feeder watches (the next most commonly recorded species were blue tit *Cyanistes caeruleus* [recorded at feeders during 42% of all watches] and great tit *Parus major* [35%]). Phase one of the study tested whether invertebrate availability limited reproductive success and colony growth, and has been reported previously (Peach et al. 2015). Here we focus on phase two of the study which tested whether year-round food availability (invertebrate prey during the breeding season plus year-round seed) limited overwinter survival and colony growth.

Measuring sparrow abundance and survival

Abundance of territorial male sparrows was assessed through two morning surveys conducted at each colony between mid-March and mid-May during 2005–2009 (see Peach et al. (2015) for full details). Surveys covered a fixed 'core' area centred on colony nesting sites and extending 50 m beyond the locations of all territorial males during the first survey year (mean core area = 1.7 ha), plus a surrounding buffer extending 200 m beyond the core area (mean area of core plus buffer = 25.4 ha). Each survey involved one of five trained observers walking a predetermined route following all accessible rights of way plus a fixed set of private gardens, and distinguishing 'chirping' territorial males from non-chirping males and females (de Laet et al. 2011). Maximum counts of chirping males in core survey areas (MCM_c) provided a year-specific measure of 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}).

As most nest sites were inaccessible, we used age ratios (counts of fledgling sparrows relative to MCM_c) as an indirect measure of sparrow reproductive success. Between mid-May and mid-August during 2005–2008, three surveys of fledgling sparrows were conducted at monthly intervals at each colony. Trained observers slowly walked a predetermined transect route within core areas and used a variety of calls and adult behavioural cues to locate and distinguish recently fledged sparrows from older juveniles. Our indirect measure of reproductive success for each colony in each year was the aggregate count of fledglings (summed across the three surveys) divided by MCM_c (see Peach et al. (2013, 2015) for validatory support of this metric).

During the winters of 2007–08 and 2008–09 we conducted mark-resighting studies at six study sites (4 fed, 2 unfed) in order to measure overwinter survival. Sparrows were trapped in domestic gardens using mist-nets and individually marked with a single metal ring plus three plastic colour rings. Sampling was conducted at monthly intervals starting in September and continuing until the following March. Each sampling occasion entailed a 6-h capture session followed over the next 2 days by a standardised resighting survey that involved trained observers walking all accessible routes within the core plus 200 m buffer area recording all colour-ringed sparrows.

Measuring potential environmental correlates of sparrow abundance

In an attempt to identify potential cross-colony correlates of sparrow abundance we recorded a suite of habitat and environmental variables across all 66 study sites (described in Table 1). As potential correlates of sparrow reproductive success we mapped the total area of domestic gardens (GARDE) and green space (parks, amenity grassland and roadside grass verges; GREEN) within core survey areas plus a 50 m surrounding buffer. Within core areas only we also mapped the extent of three fine-scale habitat features known to be frequently utilised by foraging sparrows during the breeding season in suburban areas (Vincent 2006). An index of woody vegetation volume (WOODY) was derived by summing categorical scores for scrub (height x width categories where <2 m = 1, 2–5 m = 3, >5 m = 5, within 5 m sections of hedge or garden border), trees (>5 m tall; small = 5, medium = 7.5, large = 10) and patches of bramble *Rubus* spp. or *Buddleia* spp. ($<20\ m^2 = 20$, $20–100\ m^2 = 60$, $>100\ m^2 = 100$). Areas of potentially weed-rich (wasteland, brownfield, allotments, tilled ground; SEEDY) and insect-rich habitats (grassland and ruderal vegetation; GRASS) were also mapped. We measured the density of residential buildings (HOUSE) within core survey areas using 2007 satellite images (Google Earth, Google Inc., USA) after excluding any green or brown space.

Habitat character at the wider core plus 200 m scale was described using the remotely sensed CEH Land Cover Map (LCM) from 2000 (Fuller et al. 2002). Seventeen LCM habitat categories were combined into five aggregate categories (woodland, grassland, disturbed land, wetland and urban) which were subject to a principal components analysis. The first principal component (PCA1) explained 38% of the variation and provided a measure of managed non-urban land (being negatively correlated with urban area ($r = -0.67$) and positively correlated with the extent of grassland (0.58) and disturbed land (0.42)). The second axis (PCA2) accounted for a further 21% of the variation and reflected the local extent of wetland (0.72) and woodland (0.58).

Environmental variables included the level of background supplementary feeding (BFEED) and the density of domestic cats (CAT) both estimated from surveys of local residents. At each colony we attempted to conduct face-to-face questionnaire interviews at every property within the core survey area. If the residents were out, a questionnaire was posted with a

Table 1 Potential covariates of house sparrow abundance measured at each of the 66 breeding colonies in Greater London

Category	Label	Description	Scale measured	Year(s)	Median (Range)
Habitat	GARDE	% cover domestic garden	Core +50 m	2007	38 (1–66)
Habitat	GREEN	% cover open green space (amenity grass, parks, grass verges)	Core +50 m	2007	5 (0–40)
Habitat	PCA1	1st PCA axis of LCM2000 (reflects extent of grassland & disturbed land)	Core +200 m	2000	−0.55 (−1.27–6.21)
Habitat	PCA2	2nd PCA axis of LCM2000 (reflects extent of wetland & woodland)	Core +200 m	2000	−0.38 (−2.06–4.81)
Habitat	HOUSE	Density of residential properties (per ha)	Core	2007	28.8 (7.6–71.3)
Habitat	WOODY	Index of woody vegetation volume (trees & shrubs)	Core	2006	946 (218–3052)
Habitat	GRASS	Extent (ha) of grassland (mown, unmown, ruderal vegetation)	Core	2006	0.03 (0–0.50)
Habitat	SEEDY	Extent (ha) of seed-rich habitat (tilled land, brownfield, allotment)	Core	2006	0.10 (0–0.58)
Feeding	BFEED	Index of background supplementary feeding (residents questionnaire)	Core	2006	174.4 (24.4–420.2)
Predator	CAT	Density of domestic cats (per ha; residents questionnaire)	Core	2006	7.7 (0–25.9)
Predator	HAWK	Number of bird surveys during which sparrowhawk recorded	Core +200 m	2006–09	2 (0–7)
Pollutant	NO2	Nitrogen dioxide concentration (dispersion model; $\mu g\ m^{-3}$)	Core	2004	35.2 (29.6–47.2)
Pollutant	EMR	Median electromagnetic radiation score (V/m)	Core +50 m	2008	69.5 (21–675)
Socio-econ	SODEP	Socio-economic deprivation index (weighted mean rank; low = deprived)	Core +50 m	2007	13,814 (2655– 30,480)

The scale and timing of measurement are listed along with the cross-colony median (and range) scores. General habitat descriptions were either mapped manually at the core +50 m scale (and related to fledgling abundance: GARDE & GREEN) or derived from the CEH Land Cover Map 2000 at the core +200 m scale (and related to adult male abundance: PCA1 & 2). All other variables were related to counts of both fledgling and adult male sparrows

return address. Of the 1750 completed questionnaires, 80% were completed face-to-face, with a mean of 26.5 returns per colony (range 16–46), equivalent to 51% of all households (range 22–94%). Residents were asked how many cats they owned and details of the type and frequency of any supplementary food provision. We adopted the method of Baker et al. (2008) to allow for differential cat reporting rates between face-to-face and postal returns (see Peach et al. (2013) for details). To provide an index of background supplementary feeding we multiplied a measure of the scale of provision (score for each large feeder or bird table = 2; small feeder, fatballs or bread = 1) by the frequency of provision (1 = continuous provision; 0.75 = food available on more than 50% of days; 0.5 = food available on less than 50% of days) at each household. We then multiplied the mean of these household scores by the number of households within the core survey area. A relative measure of local Sparrowhawk activity (HAWK) was provided by the proportion of all sparrow surveys conducted during 2006–2009 ($n = 17$) on which at least one Sparrowhawk was recorded.

Ground level nitrogen dioxide (NO_2) measures were derived from a kernel-based pollution dispersion model (King College's Air Pollution Toolkit) which combines point measures, traffic flows and emissions with hourly meteorological data to predict air pollution levels at a 20 m-grid resolution across London (Tonne et al. 2008). The model predicts average annual NO_2 levels at this scale with a high level of accuracy ($R^2 = 0.76$, root mean square error = 14%) and outputs from a similar dispersion model predict variation in lichen diversity on individual trees across London (Davies et al. 2007). We used predicted annual mean NO_2 levels for a single (typical) calendar year (2004) averaged across all grid points within core survey areas (mean = 30.7 points per study site), a measure that was strongly correlated (across study sites) with identical data for 2003 ($r = 0.98$, $P < 0.0001$) and a similar predicted measure of small particulate matter for 2004 ($r = 0.94$, $P < 0.0001$). Electromagnetic radiation (EMR) was measured at each colony between 11:00 and 14:00 on week days (Monday to Friday) during June–July 2008. Maximum (peak hold) electric field strength (V/m) over a 2-min period was recorded at 50-m intervals along the entire fledgling transect route (mean 23.4 readings per site, range 16–33). Measurements were based on the downlink frequencies of GSM 900/1800 MHz (925–960 MHz, 1805–1880 MHz) using a calibrated high-frequency spectrum analyser (ROM Elektronik RF survey meter, model HFR-4 s/n 262,808) with calibrated EMC directional antenna which was rotated around 360-degrees to ensure a maximum measure. Finally we used published indices of social deprivation (Noble et al. 2006) to test whether sparrows were more abundant in socially deprived localities (as proposed by Shaw et al. (2008)). For each colony we calculated a mean rank index of multiple deprivation for 2007 weighted by the area of each lower super output area (the scale at which deprivation is measured) within each core plus 50 m buffer (SODEP).

Statistical analysis

We used generalised linear mixed models (GLMMs) with Poisson distributions to test whether supplementary feeding influenced the abundance of fledglings or territorial male House Sparrows. COLONY was declared as a random term, and where necessary COLONY*YEAR to deal with over-dispersion. The fledgling GLMM took the annual aggregate core count of fledglings as the dependent variable, and specified the natural logarithm of MCM_c as an offset term to provide a per capita measure of fledgling abundance. Two nuisance variables were included as fixed effects: OBSERVER (5-level factor) and the proportion of MCM_{cb} counts in the 200 m buffer (MCM_b/MCM_{cb} or 'PBUFF') to allow for fledglings originating from nests in the 200 m buffer being recorded in the core area following local dispersal (Peach et al. 2015). Initially we tested for an effect of supplementary feeding on fledgling counts by including the terms FED (fed, unfed), YEAR (4-level factor: 2005–08) and colony SIZE (small, medium, large) and all possible interactions. In order to test whether any effect of supplementary feeding on fledgling abundance changed following the introduction of seed in May 2007, the term YEAR was replaced by the term PERIOD (before/after the introduction of seed), and the interaction FED*PERIOD tested for a change in any response to feeding following the introduction of seed (after the removal of a non-significant SIZE*FED interaction).

We tested for effects of supplementary feeding on counts of territorial males at the core plus 200 m scale using a GLMM in which MCM_{cb} was the dependent variable, COLONY was a random term, and OBSERVER, YEAR, feeding treatment (FED) and density of territorial males (DEN) in the first survey year were fixed effects, with all interactions involving YEAR, FED and DEN. A different analytical approach was required to test for any additive effect of seed provision on MCM_{cb} counts in 2008 and 2009. For this we included fixed effects for OBSERVER, YEAR, FED and FED*DEN to allow for a density-dependent effect of mealworm provision on MCM_{cb} (Peach et al. 2015). To test for an additive effect of seed provision, we included a two-level factor (SEED) that was coded '0' for all colonies during 2005–2007, and '1' for all fed colonies during 2008 and 2009. We checked whether any effect of experimental seed provision was modified by the level of background supplementary feeding measured at each colony by adding a three-level factor (BFEEDC) reflecting high, medium and low levels of background feeding by residents (three equal divisions of BFEED), and its interaction with SEED. Finally, we tested whether changes in MCM_{cb} were related to the observed seed consumption rate (high, medium, low: SEEDC) with and without the BFEEDC term allowing for variation in background feeding across study colonies. Seed consumption rate at each colony was estimated by multiplying total seed provision over the 23 month feeding period by the proportion of 15-min feeder watches (total number of watches = 2885, range = 13–473 per colony) during which house sparrows were observed feeding on our sunflower hearts (mean = 0.783, range = 0.299–1.000).

We tested for relationships between habitat/environmental variables and cross-colony variation in (i) per capita fledgling abundance, (ii) the density of territorial males before the introduction of our supplementary feeding, and (iii) linear temporal trends in counts of territorial males between 2005 and 2009. Fledgling abundance was measured at the core colony scale, and involved screening variables recorded mainly at the same or slightly coarser scale of core plus 50 m (Table 1). Adult male abundance was analysed at the core plus 200 m scale, and involved screening variables measured at the core and wider scales (Table 1). Over the 5 years of surveys, 27% of all recorded territorial males were located within core survey areas, the rest in the 200 m buffer. In each analysis we started with a base model that included all important terms associated with study design and supplementary feeding, and in a first step screened a set of habitat variables to identify any important predictors of sparrow abundance. In a second step we screened a set of environmental variables (urban stressors) that might plausibly have limited sparrow abundance. At each step, all candidate variables were added to the base model and backwards deletion was used to remove the least significant predictors of sparrow abundance one-by-one. Any significant habitat predictors identified in step one were retained in step two irrespective of any changes in statistical significance to ensure any relationships involving urban stressors were robust to any underlying habitat effects. Correlations between habitat and environmental variables were generally weak with only five out of 91 exceeding 0.4, and 3 exceeding 0.5 (Online Resource 1, Table A1). Stepwise deletion has been shown to perform as well as other model selection methods including information theoretic approaches (Murtaugh 2009) and gave us the flexibility to retain non-significant terms (e.g. relating to study design or habitat) and to test for interactions (see below).

The base GLMM for fledgling abundance included the terms OBS, PBUFF, YEAR, SIZE, FED and YEAR*SIZE, as well as random COLONY and COLONY*YEAR terms. As our feeding treatment affected fledgling abundance (see Results), we checked all significant predictors for interactions with FED. Generalised linear models (GLMs) were used to analyse cross-colony variation in male sparrow abundance. The dependent variable for male density was the observed count of territorial males at the core +200 m scale (MCM_{cb}) before supplementary feeding began (in either 2005 or 2006) corrected for the effects of observer (taken from the GLMM of adult abundance, above), divided by the survey area, and declaring a Normal error structure (no other design variables were needed). The base GLM testing for correlates of temporal trends in male abundance included the fixed effects OBS, COLONY and YEAR (defined as a linear covariate) plus an interaction between sparrow density (DEN) and year to allow for a density-dependent pattern of temporal change in colony size (Peach et al. 2015). Cross-colony correlates of trend in male abundance were tested through the addition of interaction terms between year and each habitat/environmental variable (YEAR*VAR), checking in each case for any modifying effect of local population density (YEAR*VAR*DEN).

GLMs and GLMMs were fitted using the GENMOD and GLIMMIX procedures of SAS version 9.4 (SAS Institute, Cary, NC, USA) using Wald tests to assess the significance of fixed effects and (for GLMMs) the Satterthwaite method for calculating degrees of freedom. Final models were checked for evidence of residual heteroscedasticity and influential observations.

We estimated monthly survival from our resighting data by fitting Cormack-Jolly-Seber (CJS) models which describe the encounter histories as the product of resighting and apparent survival probabilities (Lebreton et al. 1992). The data from the two winters were analysed separately. The main aim of the analysis was to test for an effect of supplementary feeding on survival but in order to maximise statistical power we first identified plausible and parsimonious model descriptions of the encounter history data. First we checked the assumptions of the CJS model by running goodness-of fit tests from program RELEASE (Lebreton et al. 1992) on encounter history data for males and females from five sites in 2007–08 and four sites in 2008–09. There was no evidence of trap-dependence (RELEASE Test 2: $\chi^2_{31} = 25.2$, $P > 0.75$ for 2007–08 & $\chi^2_{20} = 10.4$, $P > 0.95$ for 2008–09) but some evidence for an excess of transient individuals in some groups (significant test 3.SR for 4 out of 10 groups in 2007–08, and 2 out of 8 groups in 2008–09; Online Resource 1, Table A2). We dealt with transients by imposing an age structure in which survival during the first month after initial capture differed from that during all subsequent months (Williams et al. 2001). We also tested for additive and multiplicative effects of sex and site on survival, and of sex, site and time period (month) on recapture probability. In order to maximise statistical power to detect any effect of supplementary feeding, we did not consider temporal (monthly) variation in survival. Once a relatively parsimonious (low AIC) description of survival and resighting had been achieved, we added supplementary feeding to the model as an additive individual covariate (Williams et al. 2001) which tested whether apparent survival differed between fed and unfed sites. Although our approach potentially confounds supplementary feeding and any underlying site effects, the wider experimental design required the feeding treatment to be maintained across years. Fed and unfed study sites shared generally similar habitat and environmental characteristics especially for key traits like the extent of seed-rich habitat and background supplementary feeding (Online Resource 1, Table A3).

Results

Effects of food supplementation on fledgling abundance and overwinter survival

The overall effect of food supplementation (mealworms plus seed) on per capita fledgling abundance was significantly positive (FED: $F_{1,54} = 8.3$, $P < 0.006$) with no evidence that the effect of feeding varied between calendar years or colony sizes (Table 2). There was no evidence that the effect of feeding changed following the introduction of seed (PERIOD*FED: $F_{1,154} = 0.6$, $P > 0.4$). Supplementary feeding enhanced per capita fledging abundance by an average over the 4-year study of 55% (predicted means 1.06 vs. 1.64).

The most parsimonious CJS models were those involving age and/or sex effects on survival, and additive site, time and sex effects on resighting probability (Online Resource 1, Table A4). Adding a supplementary feeding term to the most parsimonious models indicated no difference in apparent survival between fed and unfed colonies during either winter (likelihood ratio tests: $\chi^2_1 = 0.692$, $P > 0.40$ for 2007–08 & $\chi^2_1 = 1.010$, $P > 0.30$ for 2008–09; Online Resource 1, Table A5; Fig. 1).

Effects of food supplementation on the abundance of territorial males

The effect of supplementary feeding on male abundance was density-dependent (YEAR*DEN*FED: $F_{8,\ 286} = 2.32$, $P <$ 0.02; Table 3) with a positive effect of feeding at low density colonies and a negative effect at medium density colonies

Table 2 Testing for an effect of supplementary feeding on per capita fledgling abundance during 2005–08

Model terms	*P* values		Direction
OBSERVER	0.037	0.135	
PBUFF	0.007	0.002	Positive
YEAR	0.223	–	
SIZE	0.023	0.005	
FED	0.006	0.009	Fed > Unfed
YEAR*SIZE	0.089	–	
YEAR*FED	0.802	–	
SIZE*FED	0.342	–	
YEAR*SIZE*FED	0.316	–	
PERIOD	–	0.335	
PERIOD*FED	–	0.447	

Aggregate annual fledgling count in core survey areas was the dependent variable in GLMMs with Poisson error structures and ($\log_e$) maximum counts of territorial males (MCM_c) as offset terms. Fixed effects were observer, proportion of MCM in the 200 m buffer (PBUFF), year, colony size (small, medium, large: $SIZE_{cb}$), feeding treatment (FED, unfed) and period without (2005/6) and with (2007/8) seed provision (PERIOD). Random terms were colony and colony*year

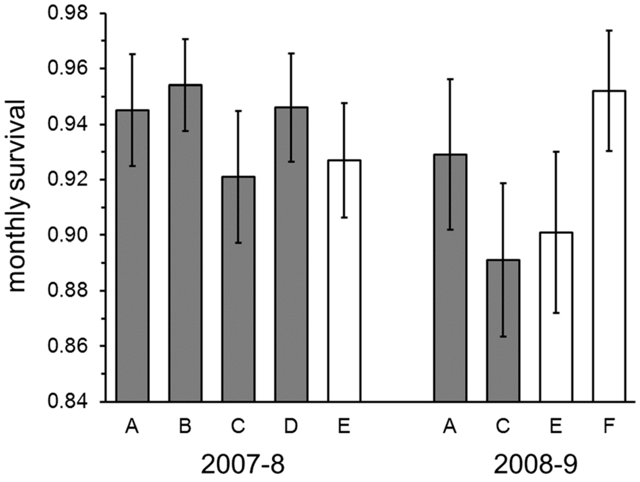

Fig. 1 Monthly overwinter survival rates (± SE) of male house sparrows at fed (filled bars) and unfed (open bars) colonies during the winters 2007–08 and 2008–09. Colonies A-D were supplementary fed with mealworms and year-round sunflower hearts, while colonies E-F were not. Survival estimates are taken from the most parsimonious models including site-specific survival parameters (Table A4)

(Fig. 2). The net impact of feeding amounted to an increase in male abundance at fed colonies of just 3.3% (based on predicted aggregate counts in 2005 and 2009 of 731.8 and 645.2 respectively at unfed colonies, and 773.5 and 705.0 at fed colonies, equivalent to 23 additional territorial males across the 33 fed colonies).

After allowing for the density-dependent effect of supplementary feeding on male abundance, there was no evidence of any additive effect of year-round seed provision (Table 4). This was true when seed provision was defined as a two-level factor (model A, Table 4), and as a three-level seed consumption rate (model C), and after allowing for cross-colony variation in the extent of background feeding (models B & D, Table 4).

Table 3 Testing for an effect of supplementary feeding on the abundance of territorial male sparrows (MCM_{cb}) during 2005–09

Model terms	*P* values	Direction
OBSERVER	0.005	
YEAR	0.319	
DEN	0.001	H > M > L
FED	0.677	
YEAR*DEN	0.001	Fig. 2
YEAR*FED	0.509	
DEN*FED	0.148	
YEAR*DEN*FED	0.019	Fig. 2

Table entries show *P* values from Wald tests, and the direction of significant fixed effects from a GLMM including the following fixed effects: OBSERVER, YEAR, initial chirping male density (low (L), medium (M), high (H): DEN), feeding treatment (FED) and all interactions between year, FED and DEN

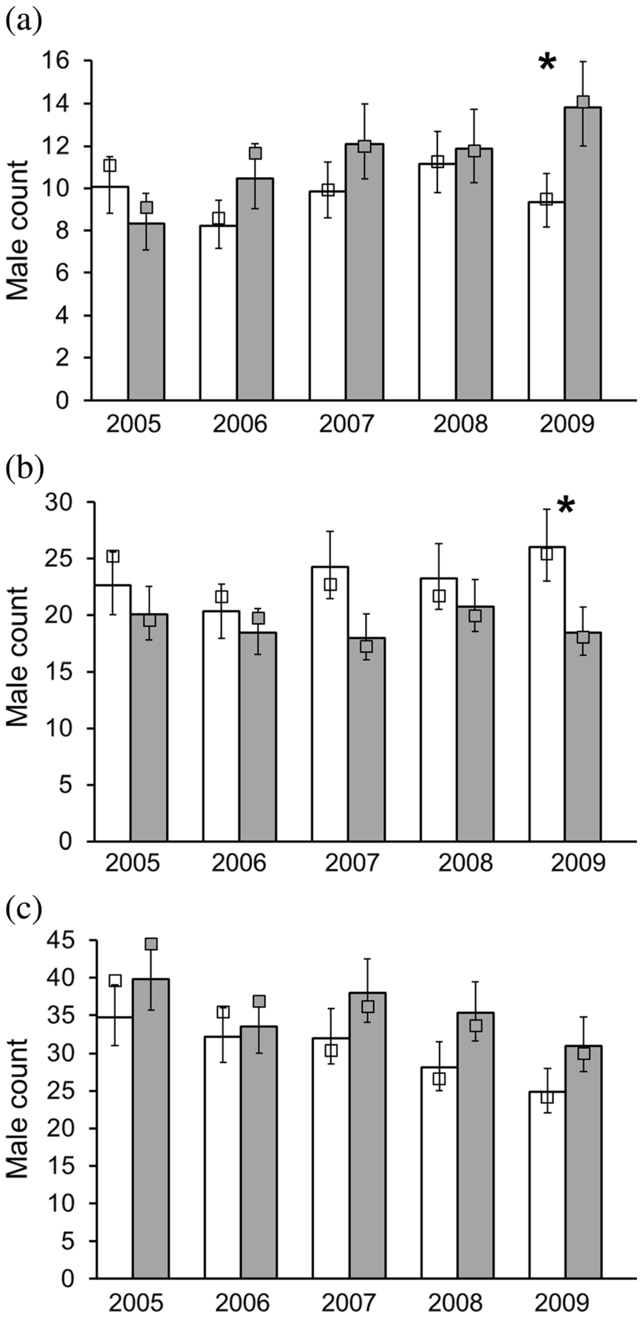

Fig. 2 Mean maximum counts of chirping males during 2005–09 within core-plus-200 m buffer areas in colonies of low (**a**), medium (**b**) and high (**c**) initial density. Bars show predicted means (± SE) and square symbols show raw mean counts. Filled bars/symbols indicate fed colonies and open bars/symbols unfed colonies. * Statistically significant ($P < 0.05$) post-hoc differences between predicted means at fed and unfed colonies

Correlates of cross-colony variation in sparrow abundance

Our study colonies exhibited wide variation in habitat character, housing density, background supplementary feeding, domestic cat density, air pollution and human social deprivation (Table 1). Per capita fledgling counts

Table 4 Testing for an additive effect of seed provision on the abundance of territorial male sparrows ($\mathrm{MCM}_{\mathrm{cb}}$)

Model terms	(A) Base + Seed Provision[a]	(B) Base + Background Feeding	(C) Base + Consumption	(D) Base + Consumption + Background Feeding
OBSERVER	0.043	0.059	0.026	0.056
YEAR	0.291	0.311	0.267	0.268
FED	0.381	0.347	0.342	0.335
FED*DEN	<0.0001	<0.0001	<0.0001	<0.0001
SEED/SEEDC	0.556	0.600	0.137[b]	0.159[b]
BFEEDC	–	0.130	–	0.264
BFEEDC*SEED/SEEDC	–	0.704	–	0.185[b]

Fixed effects from GLMMs are listed which include observer, year, male density (low, medium, high: DEN), supplementary feeding during 2006–09 (FED) and its interaction with male density. We test for additive effects of seed provision (model A: fed or unfed in 2008 and 2009; SEED), and allowing for any effect of background feeding (model B: low, medium, high: BFEEDC). We also test whether changes in male abundance were related to the observed seed consumption rate (high, medium, low: SEEDC) without (C) and with (D) the terms allowing for variation in background feeding across study colonies. All models include random terms for colony and colony*year. Table entries show *P* values from Wald tests

[a] The following interaction terms were not significant when added to model (A): SEED*DENSITY ($P = 0.470$); after removal of the SEED term, FED*DENSITY*YEAR ($P > 0.18$)

[b] These *P* values relate to the term SEEDC

declined as garden area and Sparrowhawk activity increased (Table 5, Fig. 3). Area of seed-rich habitat was positively related to fledgling counts at unfed colonies ($t_{55} = 2.19$, $P = 0.033$) with a weaker negative relationship ($t_{52} = -1.90$, $P = 0.063$) at fed colonies (Fig. 3), the interaction being highly significant (Table 5).

Table 5 Testing for habitat and environmental correlates of house sparrow abundance across 66 study areas in London

Fledgling abundance				Adult male density						
Independent variables	Fledgling abundance:			Independent variables	Initial male density:			Trend in male density:		
	UNI	MUL	Direction		UNI	MUL	Direction	UNI	MUL	Direction
Habitats										
GARDE	0.022	0.020	NEG	PCA1	0.022	0.022	POS	0.258	–	
GREEN	0.091	–		PCA2	0.523	–		0.742	–	
HOUSE	0.732	–		HOUSE	0.275	–		0.578	–	
WOODY	0.114	–		WOODY	0.555	–		0.293	–	
GRASS	0.121	–		GRASS	0.022	–	POS	0.630	–	
SEEDY	0.039 #	0.034	POS: unfed	SEEDY	0.456	–		0.001 #	0.001	POS: high density
Environmental										
BFEED	0.554	–		BFEED	0.048	–	POS	0.186	–	
CAT	0.436	–		CAT	0.759	–		0.521	–	
HAWK	0.038	0.038	NEG	HAWK	0.004	–	POS	0.634	–	
NO2	0.617	–		NO2	0.001	0.001	NEG	0.016 #	0.016	NEG: medium density
EMR	0.295	–		EMR	0.054	–	NEG	0.982	–	
SODEP	0.738	–		SODEP	0.401	–		0.549	–	
Final models										
Model terms	P-value			Model terms	P-value			Model terms	P-value	
GARDE	0.017			PCA1	0.306			YEAR*DEN	0.009	
SEEDY	0.927			NO2	0.001			YEAR*DEN*SEEDY	0.001	
SEEDY*FED	0.006							YEAR*DEN*NO2	0.016	
HAWK	0.038									

Fledgling abundance 2005–2008 was measured in core colony areas, while adult male density was measured in core plus 200 m buffers. Initial male density was measured before supplementary feeding began (either 2005 or 2006), and the linear trend in male density was measured between 2005 or 2006, and 2009. For fledgling abundance, independent variables were tested as a linear main effect plus an interaction with experimental feeding status (FED: fed, unfed). For trend in male density, independent variables were tested as a linear predictor (YEAR*variable) plus an interaction with adult male sparrow density (YEAR*DEN*variable, where DEN = high, medium or low). The table summarises the statistical significance (*P*-values) of univariate (UNI: one variable at a time) and multivariate (MUL: following backwards deletion) relationships (see Methods for further details). Interactive relationships are indicated by the # symbol and the *P*-value relates to the interactive term

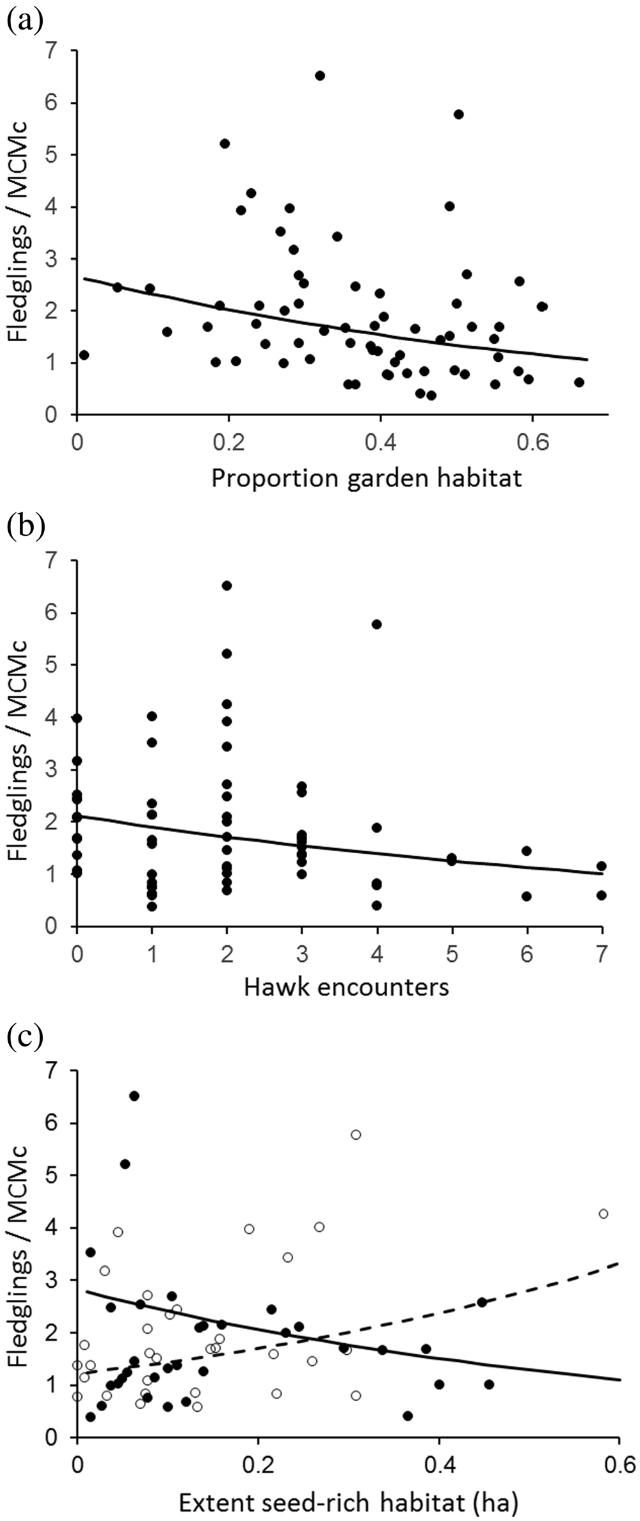

Fig. 3 Relationships between per capita fledgling abundance and (**a**) the proportional cover of domestic gardens, (**b**) Sparrowhawk activity and (**c**) the area of seed-rich habitats at fed (filled symbols) and unfed (open symbols) colonies. See Methods for variable definitions

Prior to the initiation of supplementary feeding, the density of territorial male sparrows was positively related to PCA1 (the extent of disturbed land and grassland) although this relationship was rendered non-significant by the inclusion of a strong negative relationship involving nitrogen dioxide air pollution (Table 5, Fig. 4). Temporal trends in male abundance varied significantly between colony density categories (YEAR*DEN: $F_{2,\ 244} = 24.3$, $P < 0.0001$), declining significantly at high density colonies but showing no overall trends at low and medium density colonies (Fig. 2). Both significant correlates of cross-colony variation in trends in male abundance exhibited density-dependence (Table 5). Trends in abundance at high density colonies were positively related to the area of seed-rich habitat, while trends at medium-density colonies were negatively related to nitrogen dioxide air pollution (Fig. 5).

Discussion

Effects of food supplementation

Our previous studies documented positive effects of mealworm supplementation on House Sparrow nesting success (+55%; Peach et al. (2014)), fledgling abundance (+62%) and adult male abundance in low density colonies (+36% following two seasons of feeding; Peach et al. (2015)). Similar impacts were evident over the four years of supplementary feeding considered here (fledgling abundance: +55%; adult male abundance at low density colonies: +33%) and there was no evidence of any additive effect of unlimited year-round seed provision during the third and fourth year of supplementary feeding. Given the similar magnitudes of feeding impacts on sparrow abundance before and after the introduction of seed, and the absence of any effect of feeding on overwinter survival, we conclude that the addition of unlimited seed to the experimental feeding treatment had no impact on sparrow demography or abundance. The large positive effect of mealworm supplementation on fledgling counts

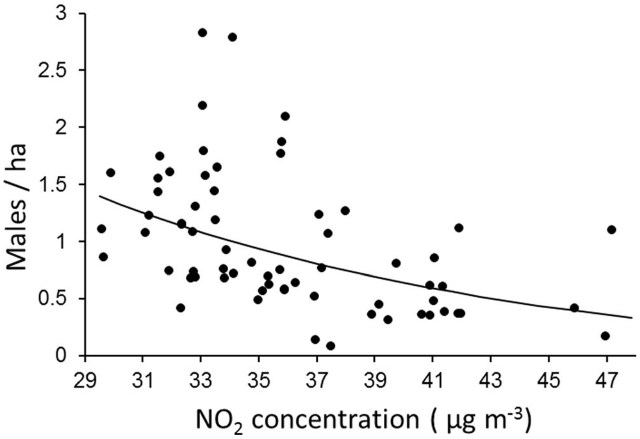

Fig. 4 Relationship between the density of territorial male sparrows and average year-round nitrogen dioxide concentration in the air. See Methods for nitrogen dioxide derivation

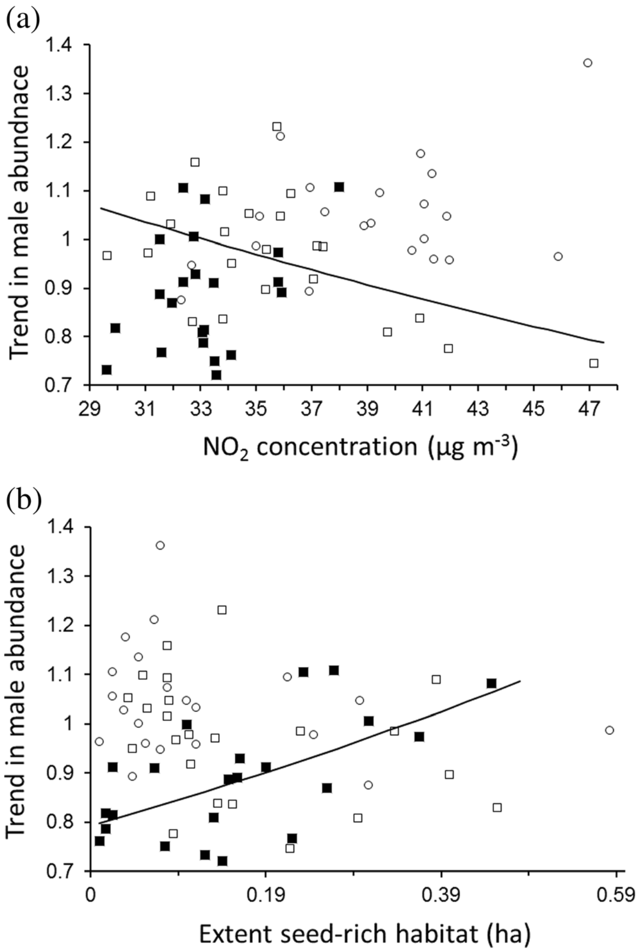

Fig. 5 Relationships between the linear trend in male abundance during 2005–09 and (**a**) average year-round nitrogen dioxide concentration at medium density colonies (open squares) and (**b**) the area of seed-rich habitats at high density colonies (filled squares). Open circles indicate low density colonies. See Methods for variable definitions

probably reflects a widespread limiting effect of invertebrate availability on House Sparrow reproductive success and chick condition in urban environments (Peach et al. 2008; Seress et al. 2012; Peach et al. 2015).

Our results clearly indicate that despite invertebrate availability limiting reproductive success, food availability more broadly (encompassing breeding season invertebrate availability and year round seed availability) does not limit the size of the suburban House Sparrow population across London. Had food availability limited the survival of young sparrows between the post-fledging period (July) and recruitment as first-time breeders (March–April), or the survival of adults, we would have expected to measure higher overwinter survival and increased abundance of territorial male sparrows at fed colonies. This is particularly true given the depleted status of our wider study population and the low rates of natal dispersal in House Sparrows particularly in suburban landscapes (i.e. any demographic impacts should have been evident locally; Fleischer et al. 1984; Paradis et al. 1998; Vangestel et al. 2011). Our conclusion that food availability limits the development and survival of urban House Sparrow chicks but not fully grown birds (after July of the first summer of life) is consistent with the age related impacts of urbanisation reported for sparrow tarsus length and feather quality (Meillere et al. 2017). The absence of any post-fledging demographic response to our experimental food provision implies that factors unrelated to food availability probably drove the recent population decline affecting London House Sparrows.

It is important to acknowledge that background supplementary feeding was ubiquitous (albeit highly variable) across our 66 study sites (Table 1). Our study compared substantial breeding season protein supplementation (estimated to have satisfied 82% of local chick energy requirements; Peach et al. 2015) plus unlimited year-round high energy seed provision against current levels of background food provision (mainly seed, fat balls and other vegetable materials; protein supplementation was rare). It may be that current levels of background food provision are sufficient to avoid demographic limitation linked to food availability, but this does not affect our conclusion that food availability is unlikely to have caused the recent House Sparrow population decline across London. It is also unlikely that unusual weather conditions during our study might have negated or offset any potential impacts of supplementary feeding on sparrows. Of the four study summers, two were relatively wet (2007 & 2008) and one relatively dry (2005), and of the two fed winters, one was relatively mild (2007–08) and the other relatively cold (2008–09) (Online Resource 1, Table A6).

Correlates of sparrow abundance

Despite marked variation in habitat character across the 66 study colonies, our analysis identified only one habitat (seed-rich) as having a potential influence on House Sparrow abundance. Relatively high fledgling counts in unfed survey areas having large areas of wasteland, disturbed land or allotments could reflect greater usage of these seed-rich habitats at colonies lacking our supplementary feeding or perhaps higher detectability of young sparrows in these relatively accessible open habitats. However, the positive relationship between the extent of seed-rich habitat and the temporal trend in adult male abundance is more likely to reflect a genuine impact of seed-rich habitat on sparrow demography as sparrows are largely granivorous outside of the breeding season, and are known to select seed-rich and disturbed habitats for foraging (Mitschke et al. 2000; Anderson 2006; Chamberlain et al. 2007). The restriction of this relationship to high density sparrow sites might reflect a tendency for seed-rich habitat to limit sparrow demography only in localities where there may be competition for the associated seed resources. Although garden area had a negative influence on fledgling counts this relationship might simply reflect a tendency for fledglings to be under-recorded in survey areas having a high cover of privately-owned domestic gardens to which our surveyors will have had only partial access.

The negative relationship between Sparrowhawk activity and fledgling abundance could reflect genuinely lower abundance (perhaps linked to increased predation mortality) or a behavioural response of sparrows to hawk activity. Both of these interpretations also apply to a study reporting negative correlations between sparrow counts and hawk activity in UK gardens (Bell et al. 2010). Adult male density was positively related to hawk activity although this relationship disappeared when other stronger predictors of male density were included in GLMs (Table 4). Our measure of hawk activity was relatively crude and may not reliably reflect true cross-colony variation in Sparrowhawk hunting activity. All three of our sparrow density measures were unrelated to the density of domestic cats despite wide cross-colony variation in the latter (0.0–25.9 cats ha^{-1}). Previous studies have reported rates of cat depredation on rural and suburban House Sparrow populations high enough to potentially limit population size (Churcher and Lawton 1987; Thomas et al. 2012).

The relationship between the density of territorial male sparrows and local nitrogen dioxide air pollution was statistically strong and robust to any confounding effects of habitat or other potential environmental stressors (Table 4, Fig. 4). Most of the recent decline in House Sparrow abundance across London occurred prior to the commencement of this study (1995–2005: 60% decline; 1995–2015: 71% decline; unpublished Breeding Bird Survey data), so any distribution or abundance patterns relating to environmental drivers of population change should have been apparent by the start of our study in 2005. Our data also indicate more negative temporal trends in territorial male abundance at colonies subjected to higher levels of air pollution albeit restricted to colonies of intermediate initial density (Fig. 5). Anthropogenic air pollutants like nitrogen dioxide and trace metals are known to have a variety of impacts on the physiology and health status of a wide range of vertebrates including birds, mammals and humans (Isaksson 2010; Koivula and Eeva 2010). Prolonged exposure to air pollutants can cause oxidative stress and inflammation leading to tissue damage linked to disease and senescence (Isaksson 2015). Oxidative stress is negatively associated with several avian fitness traits including immune response, reproduction and survival (Costantini 2008). House Sparrows from more urbanised localities have higher physiological indicators of oxidative stress (haemoglobin and total antioxidant capacity) than their rural counterparts (Herrera-Duenas et al. 2014), and higher levels of lead in feathers was associated with a higher prevalence of avian malaria *Plasmodium relictum* (Bichet et al. 2013). Furthermore, House Sparrow nests in localities with higher levels of air pollution contained chicks in poorer condition and with smaller tarsi (Peach et al. 2008). The correlations reported here between air pollution and sparrow breeding density, and trends in breeding density, suggest some component (or correlate) of air pollution may be affecting the fitness of this species in urban landscapes and thereby contributing to ongoing population declines.

Conclusions

This study conclusively demonstrates that food availability is not limiting an extensive declining suburban sparrow population. Increasing food availability is unlikely on its own to lead to any recovery of the London sparrow population. However, the availability of invertebrate prey limits reproductive success and chick development in urban House Sparrows and management to increase invertebrate availability may therefore be beneficial as part of a wider package of conservation measures. This study supports previous work in providing evidence for the benefits to sparrows of seed-rich habitats like allotments and disturbed land (Chamberlain et al. 2007) and such habitats should be maintained and provided where absent. Finally, this study provides correlative evidence of negative impacts of air pollution on sparrow abundance, and given the growing concerns about air pollution impacts on human health in many modern cities, this issue merits further investigation.

Acknowledgements We are indebted to the residents of London who allowed access to their gardens and put out supplementary food each day. We are grateful to Howard Vaughan and Daria Dadam who helped with fieldwork, to Anne-Marie Knight (LiveFoodsDirect Ltd.) who managed mealworm deliveries to volunteers, and to Adam Butler and David Elston (BioSS) for statistical advice. We thank David Dajnak (Environmental Research Group, Kings College, London) for providing air pollution data, and Isaac Jamieson (Imperial College, London) for the loan of an EMR spectrum analyser and sampling advice. The study was funded by the Royal Society for the Protection of Birds.

References

Anderson TR (2006) Biology of the ubiquitous house sparrow. Oxford University Press, Oxford

Baker PJ, Molony SE, Stone E, Cuthill IC, Harris S (2008) Cats about town: is predation by free-ranging pet cats likely to affect urban bird populations. Ibis 150(Suppl. 1):86–99

Barber JR, Crooks KR, Fristrup KM (2009) The costs of chronic noise exposure for terrestrial organisms. Trends Ecol Evol 25:180–189

Bell CP, Baker SW, Parkes NG, de L. Brooke M, Chamberlain DE (2010) The role of the Eurasian sparrowhawk (*Accipiter nisus*) in the decline of the house sparrow (*Passer domesticus*) in Britain. Auk 127:411–420

Bichet C, Scheifler R, Coeurdassier M, Julliard R, Sorci G, Loiseau C (2013) Urbanization, trace metal pollution and malaria prevalence in the house sparrow. PLoS One 8(1):e53866

Bonnington C, Gaston KJ, Evans KL (2013) Fearing the feline: domestic cats reduce avian fecundity through trait-mediated indirect effects that increase nest predation by other species. J Appl Ecol 50:15–24

Bradley CA, Altizer S (2007) Urbanization and the ecology of wildlife diseases. Trends Ecol Evol 22:95–102

Brichetti P, Rubolini D, Galeotti P, Fasola M (2008) Recent declines in urban Italian sparrow (*Passer domesticus italiae*) populations in northern Italy. Ibis 150:177–181

Brittingham MC, Temple SA (1988) Impacts of supplementary feeding on survival rates of black-capped chickadees. Ecology 69:581–589

Chamberlain DE, Toms MP, Cleary-McHarg R, Banks AN (2007) House sparrow habitat use in urbanized landscapes. J Ornithol 148:453–462

Chamberlain DE, Cannon AR, Toms MP, Leech DI, Hatchwell BJ, Gaston KJ (2009) Avian productivity in urban landscapes: a review and meta-analysis. Ibis 151:1–18

Chase JF, Walsh JJ (2006) Urban effects on native avifauna: a review. Landsc Urban Plan 74:46–69

Churcher PB, Lawton JH (1987) Predation by domestic cats in an English village. J Zool (Lond) 212:439–455

Clergeau P, Croci S, Jokimaki J, Kaisanlahti-Jokimaki M-L, Dinnetti M (2006) Avifauna homogenisation by urbanisation: analysis at different European latitudes. Biol Conserv 127:336–344

Costantini D (2008) Oxidative stress in ecology and evolution: lessons from avian studies. Ecol Lett 11:1238–1251

Dandapat A, Banerjee D, Chakraborty D (2010) The case of the disappearing house sparrow (*Passer domesticus indicus*). Vet World 3:97–100

Davies L, Bates JW, Bell JNB, James PW, Purvis OW (2007) Diversity and sensitivity of epiphytes to oxides of nitrogen in London. Environ Pollut 146:299–310

De Laet J, Peach WJ, Summers-Smith JD (2011) Protocol for censusing urban sparrows. Brit Birds 104:255–260

Erskine AJ (2006) Recent declines of house sparrows in Canada's maritime provinces. Can Field Nat 120:43–49

Everaert J, Bauwens D (2007) A possible effect of electromagnetic radiation from mobile phone base stations on the number of breeding house sparrows. Electromagn Biol Med 26:63–72

Fleischer RC, Lowther PE, Johnston RF (1984) Natal dispersal in house sparrows: possible causes and consequences. J Field Ornithol 55: 444–456

Fuller RM, Smith GM, Sanderson JM, Hill RA, Thomson AG, Cox R, et al (2002) Countryside Survey 2000 module 7: Land cover map 2000. Centre for Ecology & Hydrology, NERC, UK

Gaston KJ, Bennie J, Davies TW, Hopkins J (2013) The ecological impacts of nighttime light pollution: a mechanistic appraisal. Biol Rev 88:912–927

Grimm NB, Faeth SH, Golubiewski NE, Redman CL, Wu J, Bai X et al (2008) Global change and the ecology of cities. Science 319(5864): 756–760

Hanmer HJ, Thomas RL, Fellowes MDE (2017) Provision of supplementary food for wild birds may increase the risk of local nest predation. Ibis 159:158–167

Heij CJ, Moeliker CW (1990) Population dynamics of Dutch house sparrows in urban, suburban, and rural habitats. In: Pinowski J, Summers-Smith JD (eds) Graniovorous birds in the agricultural landscape. PWN-polish scientific. Publishers, Warsaw, pp 59–85

Herrera-Duenas A, Pineda J, Antonio MT, Aguirre JI (2014) Oxidative stress of house sparrow as bioindicator of urban pollution. Ecol Indic 42:6–9

Hole DG, Whittingham MJ, Bradbury RB, Anderson GQA, Lee PLM, Wilson JD, Krebs JR (2002) Widespread local house sparrow extinctions. Nature 418:931–932

Isaksson C (2010) Pollution and its impact on wild animals: a meta-analysis on oxidative stress. EcoHealth 7:342–350

Isaksson C (2015) Urbanization, oxidative stress and inflammation: a question of evolving, acclimatizing or coping with urban environmental stress. Funct Ecol 29:913–923

Isaksson C, Anderson S (2007) Carotenoid diet and nestling provisioning in urban and rural great tits. J Avian Biol 38:564–572

Jones DN, Reynolds SJ (2008) Garden bird feeding: a global research opportunity. J Avian Biol 39:265–271

Kelly FJ (2003) Oxidative stress: its role in air pollution and adverse health effects. Occup Environ Med 60:612–616

Koivula MJ, Eeva T (2010) Metal related oxidative stress in wild birds. Environ Pollut 158:2359–2370

Lebreton J-D, Burnham KP, Clobert J, Anderson DR (1992) Modelling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecol Monogr 62:67–118

London Assembly (2005). Crazy paving: the environmental importance of London's front gardens. Greater London Authority, London, UK. https://www.london.gov.uk/about-us/london-assembly/london-assembly-publications/crazy-paving-environmental-importance-londons. Accessed 23 March 2018

London Assembly (2007). Chainsaw massacre: a review of London's street trees. Greater London Authority, London, UK. https://www.london.gov.uk/about-us/london-assembly/london-assembly-publications/chainsaw-massacre-review-londons-street-trees. Accessed 23 March 2018

McKinney ML (2008) Effects of urbanisation on species richness: a review of plants and animals. Urban Ecosyst 11:161–176

Meillere A, Brischoux F, Henry P-Y, Michaud B, Garcin R, Angelier F (2017) Growing in a city: consequences of body size and plumage quality in an urban dweller, the house sparrow. Landsc Urban Plan 160:127–138

Mitschke A, Rathje H, Baumung S (2000) House sparrows in Hamburg: population habitat choice and threats. Hamburger Avifaunist Beitr 30:129–204

Murgui E, Macias A (2010) Changes in the house sparrow population in Valencia (Spain) from 1998-2008. Bird Study 57:281–288

Murtaugh PA (2009) Performance of several variable-selection methods applied to real ecological data. Ecol Lett 12:1061–1068

Noble M, Wright G, Smith G, Dibben C (2006) Measuring multiple deprivation at the small-area level. Environ Plan A 38:169–185

Paradis E, Baillie SR, Sutherland WJ, Gregory RD (1998) Patterns of natal and breeding dispersal in birds. J Anim Ecol 67:518–536

Pauleit S, Ennos R, Golding Y (2005) Modeling the environmental impacts of urban land use and land cover change – a study in Merseyside, UK. Landsc Urban Plan 71:295–310

Peach WJ, Vincent KE, Fowler JA, Grice PV (2008) Reproductive success of house sparrows along an urban gradient. Anim Conserv 11: 493–503

Peach WJ, Mallord JW, Orsman CJ, Ockendon N, Haines WG (2013) Testing assumptions of a supplementary feeding experiment aimed at suburban house sparrows. Bird Study 60:308–320

Peach WJ, Sheehan DK, Kirby WB (2014) Supplementary feeding of mealworms enhances reproductive success in garden nesting house sparrows. Bird Study 61:378–385

Peach WJ, Mallord JW, Ockendon N, Orsman CJ, Haines WG (2015) Invertebrate prey availability limits reproductive success but not breeding population size in suburban house sparrows. Ibis 157: 601–613

Pickett STA, Cadenasso ML, Grove JM, Boone CG, Groffman PM, Irwin E et al (2011) Urban ecological systems: scientific foundations and a decade of progress. J Environ Manag 92:331–362

Plummer KE, Bearhop S, Leech DI, Chamberlain DE, Blount JD (2013) Winter food provisioning reduces future breeding performance in a wild bird. Sci Rep 3:2002. https://doi.org/10.1038/srep02002

Raven MJ, Noble DG, Baillie SR (2007) The breeding bird survey 2006. British Trust for Ornithology, Thetford, UK. https://www.bto.org/sites/default/files/u16/downloads/reports/bbsreport06.pdf. Accessed 23 March 2018

Ringsby TH, Saether BE, Solberg EJ (1998) Factors affecting juvenile survival in house sparrow. J Avian Biol 29:241–247

Robb GN, McDonald RA, Chamberlain DE, Bearhop S (2008) Food for thought: supplementary feeding as a driver of ecological change in avian populations. Front Ecol Environ 6:476–484

Robinson RA, Lawson B, Toms MP, Peck KM, Kirkwood JK, Chantrey J et al (2010) Emerging infectious disease leads to rapid population declines of common British birds. PLoS One 5(8):e12215. https://doi.org/10.1371/journal.pone.0012215

Schroeder J, Nakagawa S, Cleasby IR, Burke T (2012) Passerine birds breeding under chronic noise experience reduced fitness. PLoS One 7(7):e39200

Schwagmeyer PL, Mock DW (2008) Parental provisioning and offspring fitness: size matters. Anim Behav 75:291–298

Seress G, Bokony V, Pipoly I, Szep T, Nagy K, Liker A (2012) Urbanization, nestling growth and reproductive success in a moderately declining house sparrow population. J Avian Biol 43:403–414

Shaw LM, Chamberlain D, Evans M (2008) The house sparrow *Passer domesticus* in urban areas: reviewing a possible link between post-decline distribution and human socio-economic status. J Ornithol 149:293–299

Shochat E, Warren PS, Faeth SH, McIntyre NE, Hope D (2006) From patterns to emerging processes in mechanistic urban ecology. Trends Ecol Evol 21:186–191

Summers-Smith JD (2003) The decline of the house sparrow: a review. Brit Birds 96:439–446

Summers-Smith JD (2007) Is unleading petrol a factor in urban house sparrow decline? Brit Birds 100:558–559

Thomas RL, Fellowes MDE, Baker PJ (2012) Spatio-temporal variation in predation by urban domestic cats (*Felis catus*) and the acceptability of possible management actions in the UK. PLoS One 7(11): e49369. https://doi.org/10.1371/journal.pone.0049369

Tonne C, Beevers S, Armstrong B, Kelly F, Wilkinson P (2008) Air pollution and mortality benefits of the London congestion charge: spatial and socioeconomic inequalities. J Occup Environ Med 65: 620–627

Vangestel C, Mergeay J, Dawson DA, Vandomme V, Lens L (2011) Spatial heterogeneity in genetic relatedness among house sparrows along an urban-rural gradient as revealed by individual-based analysis. Mol Ecol 20:4643–4653

Vincent KE (2006). Investigating the causes of the decline of the urban house sparrow population in Britain. PhD thesis, De Montfort University, Leicester, UK. http://www.katevincent.org/. Accessed 21 March 2018

Williams BK, Nichols JD, Conroy MJ (2001) Analysis and management of animal populations. Academic Press, San Diego