

# Urban Ecosystems

## Depleted suburban House Sparrow *Passer domesticus* population not limited by food availability --Manuscript Draft--

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<b>Corresponding Author:</b>	Will Peach Royal Society for the Protection of Birds Sandy, Beds UNITED KINGDOM	
<b>Corresponding Author Secondary Information:</b>		
<b>Corresponding Author's Institution:</b>	Royal Society for the Protection of Birds	
<b>Corresponding Author's Secondary Institution:</b>		
<b>First Author:</b>	Will Peach	
<b>First Author Secondary Information:</b>		
<b>Order of Authors:</b>	Will Peach	
	John Mallord	
	Nancy Ockendon	
	Chris Orsman	
	William Haines	
<b>Order of Authors Secondary Information:</b>		
<b>Funding Information:</b>	Royal Society for the Protection of Birds	Dr Will Peach
<b>Abstract:</b>	<p>Little is known about the environmental factors that limit the demography and abundance of wild vertebrates in highly modified urban environments. The House Sparrow <i>Passer domesticus</i> 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.</p>	

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4 Title: Depleted suburban House Sparrow *Passer domesticus* population not limited by food  
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11 Will J. Peach<sup>1\*</sup>, John W. Mallord<sup>1</sup>, Nancy Ockendon<sup>1</sup>, Chris J. Orsman<sup>1</sup> & William G Haines<sup>1</sup>  
12  
13  
14

15 1. RSPB Centre for Conservation Science, RSPB, The Lodge, Sandy, Bedfordshire SG19 2DL,  
16  
17

18 United Kingdom  
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22 \*Corresponding author. RSPB Centre for Conservation Science, RSPB, The Lodge, Sandy,  
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25 Bedfordshire SG19 2DL, United Kingdom. Tel: 00 44 1767 693259. E-mail:  
26  
27

28 [will.peach@rspb.org.uk](mailto:will.peach@rspb.org.uk).  
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## 34 **Abstract**

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40 vertebrates in highly modified urban environments. The House Sparrow *Passer domesticus* is a  
41 globally widespread species whose urban populations have recently undergone substantial  
42 declines particularly in Europe. The environmental drivers of these declines remain unknown. In  
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44 reproductive success but not population size in a suburban sparrow population. In this study we  
45 test experimentally whether year-round food availability limits demography and population size.  
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47 plus unlimited high-energy seed (year-round) at 33 sparrow colonies spread across suburban  
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16 pollution. Sparrows were more abundant, or showed more positive temporal changes in  
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## 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).

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4 The House Sparrow *Passer domesticus* is a globally widespread urban-adapted species  
5  
6 (Anderson 2006). In recent decades, evidence has emerged of substantial House Sparrow  
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8 population declines in urban centres across Europe, Canada and India (Summers-Smith 2003;  
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10 Erskine 2006; Shaw et al. 2008; Dandapat et al. 2010; Murgui and Macias 2010). For example,  
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12 House Sparrow numbers declined by 60% across London during 1994-2006, and by 50% in the  
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14 towns and cities of Lombardy, northern Italy during 1996-2006 (Raven et al. 2007; Brichetti et  
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16 al. 2008). Environmental causes of these declines remain obscure but a variety of candidate  
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18 drivers have been proposed. These include increased depredation associated with Sparrowhawks  
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20 *Accipiter nisus* or domestic cats (Bell et al. 2010; Thomas et al. 2012), effects of air pollutants or  
21  
22 electromagnetic radiation from telephone masts (Everaert and Bauwens 2007; Summers-Smith  
23  
24 2007), and nutritional constraints during reproduction (Peach et al. 2008; Seress et al. 2012).  
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26 Invertebrates dominate the diets of House Sparrow chicks (Anderson 2006), and nestlings fed  
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28 larger prey items tend to weigh more at fledging and are more likely to survive to recruit as  
29  
30 breeding adults (Ringsby et al. 1998; Schwagmeyer and Mock 2008). A shortage of suitable  
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32 invertebrate prey in urban-suburban environments could therefore affect nesting success,  
33  
34 fledgling quality and survival during the first year of life. Lack of seed food on farmland has  
35  
36 been shown to reduce the overwinter survival of House Sparrows (Hole et al. 2002) but there is  
37  
38 little information on the likelihood of seasonal seed shortages in urban landscapes. There is  
39  
40 however evidence of widespread losses of green and brown space, of trees and the conversion of  
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42 residential gardens for housing or parking (e.g. London Assembly 2005, 2007; Pauleit et al.  
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44 2005), which is likely to have reduced the availability of important sparrow foraging habitats  
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46 such as deciduous woody vegetation and grassland (Vincent 2006). It has been suggested that  
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48 such habitat changes have been concentrated into more affluent urban districts which might  
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4 account for the apparent persistence of House Sparrows in more socially deprived areas (Shaw et  
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6 al. 2008).  
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11 In this study we tested experimentally whether food availability limits the demography and  
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13 population size of a depleted suburban House Sparrow population. We previously reported that  
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15 supplementary provision of invertebrate prey during the breeding season raised nesting success  
16  
17 and fledgling abundance but had little impact on population size (Peach et al. 2015). The current  
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19 study tested whether year-round food provision (incorporating breeding season invertebrates plus  
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21 year-round high-energy seed) affected reproductive success, overwinter survival and population  
22  
23 growth. The experiment was conducted across 66 House Sparrow colonies of widely contrasting  
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25 environmental character. This variation allowed us to test whether colony-level demography,  
26  
27 density and growth were related to a range of potential urban stressors such as predator density  
28  
29 and pollution. The aim of the study was to test empirically whether food availability or other  
30  
31 potential urban stressors constitute plausible drivers of House Sparrow population change in  
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33 urban landscapes. The study is intended to inform future conservation programmes aimed at  
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35 urban sparrow populations.  
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45 Despite the global extent of anthropogenic supplementary feeding of birds (Robb et al. 2008),  
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47 our study appears to be the first experimental assessment of the demographic impact of seed  
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49 provision in an urban environment, most previous studies having been conducted in rural  
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51 landscapes where food supply is easier to manipulate (e.g. Brittingham and Temple 1988;  
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53 Plummer et al. 2013). House Sparrows are particularly suited to such a study because they  
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4 readily consume supplementary food and remain relatively sedentary throughout their annual  
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6 cycle (Fleischer et al. 1984; Heij and Moeliker 1990; Anderson 2006; Vangestel et al. 2011).  
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## 10 11 **Methods**

### 12 13 14 15 **Supplementary feeding**

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20 Supplementary feeding was conducted over four years at 66 House Sparrow colonies located  
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22 across suburban Greater London in localities dominated by residential housing, domestic gardens  
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24 and communal green space. During the first phase of the study (2005-06) supplementary feeding  
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26 was restricted to daily provision of mealworms (live *Tenebrio molitor* larvae) throughout the  
27  
28 sparrow breeding season. At each of 33 fed colonies, a fixed weight of mealworms (averaging  
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30 103g per colony) was provided daily at 2-3 feeding locations per colony between late April and  
31  
32 early August (starting in 2005 at 27 colonies, and in 2006 at a further 6). Thirty-three unfed  
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34 colonies (matched against the sample of fed colonies for geographic location, sparrow  
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36 abundance, habitat character, domestic cat *Felis catus* density and background supplementary  
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38 feeding) served as controls (see Peach et al. (2013) for further details and site map). During a  
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40 second phase of study, mealworm provision remained unchanged and was supplemented (from  
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42 late May 2007 until March 2009) by *ad libitum* year-round provision of sunflower *Helianthus*  
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44 *annuus* hearts. This energy-rich food was provided in plastic seed feeders at the same 2-3  
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46 locations per colony (usually domestic gardens) where volunteers maintained a continual supply  
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48 of seed on every day of the year. It was common for birds to remove all mealworms from  
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50 feeders within an hour of initial provision and although sunflower hearts were sometimes  
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52 exhausted at individual feeders, the deployment of multiple feeders at each colony ensured  
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4 experimental seed provision was maintained at all times. Provision of breeding season  
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6 invertebrates plus unlimited year-round seed is expected to have satisfied the major dietary  
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8 requirements of House Sparrows throughout the year (Anderson 2006) but is unlikely to have  
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10 met all micro-nutrient or natural foraging requirements.  
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16 Total provision of sunflower hearts over the 23 months of phase two averaged 228.3 kg per  
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18 colony (range 114.8 – 1032.8 kg). House Sparrows were by far the most frequent consumers of  
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20 our supplementary food accounting for 96% of all mealworms (Peach et al. 2013) and were  
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22 recorded consuming sunflower hearts during 78% of 2,885 15-minute feeder watches (the next  
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24 most commonly recorded species were blue tit *Cyanistes caeruleus* [recorded at feeders during  
25  
26 42% of all watches] and great tit *Parus major* [35%]). Phase one of the study tested whether  
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28 invertebrate availability limited reproductive success and colony growth, and has been reported  
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30 previously (Peach et al. 2015). Here we focus on phase two of the study which tested whether  
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32 year-round food availability (invertebrate prey during the breeding season plus year-round seed)  
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34 limited overwinter survival and colony growth.  
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### 43 **Measuring sparrow abundance and survival**

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48 Abundance of territorial male sparrows was assessed through two morning surveys conducted at  
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50 each colony between mid-March and mid-May during 2005-2009 (see Peach et al. (2015) for full  
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52 details). Surveys covered a fixed ‘core’ area centred on colony nesting sites and extending 50 m  
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54 beyond the locations of all territorial males during the first survey year (mean core area = 1.7  
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56 ha), plus a surrounding buffer extending 200 m beyond the core area (mean area of core plus  
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4 buffer = 25.4 ha). Each survey involved one of five trained observers walking a predetermined  
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6 route following all accessible rights of way plus a fixed set of private gardens, and distinguishing  
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8 ‘chirping’ territorial males from non-chirping males and females (de Laet et al. 2011). Maximum  
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10 counts of chirping males in core survey areas ( $MCM_c$ ) provided a year-specific measure of  
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12 colony size, which when added to maximum counts in the 200 m buffer ( $MCM_b$ ) provided a  
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14 wider measure of local breeding population size ( $MCM_{cb}$ ).  
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21 As most nest sites were inaccessible, we used age ratios (counts of fledgling sparrows relative to  
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23  $MCM_c$ ) as an indirect measure of sparrow reproductive success. Between mid-May and mid-  
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25 August during 2005-2008, three surveys of fledgling sparrows were conducted at monthly  
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27 intervals at each colony. Trained observers slowly walked a predetermined transect route within  
28  
29 core areas and used a variety of calls and adult behavioural cues to locate and distinguish  
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31 recently fledged sparrows from older juveniles. Our indirect measure of reproductive success for  
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33 each colony in each year was the aggregate count of fledglings (summed across the three  
34  
35 surveys) divided by  $MCM_c$  (see Peach et al. (2013) & Peach et al. (2015) for validity support  
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37 of this metric).  
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45 During the winters of 2007-08 and 2008-09 we conducted mark-resighting studies at six study  
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47 sites (4 fed, 2 unfed) in order to measure overwinter survival. Sparrows were trapped in domestic  
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49 gardens using mist-nets and individually marked with a single metal ring plus three plastic colour  
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51 rings. Sampling was conducted at monthly intervals starting in September and continuing until  
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53 the following March. Each sampling occasion entailed a 6-hour capture session followed over  
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4 the next 2 days by a standardised resighting survey that involved trained observers walking all  
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6 accessible routes within the core plus 200 m buffer area recording all colour-ringed sparrows.  
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## 10 11 **Measuring potential environmental correlates of sparrow abundance** 12 13 14

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16 In an attempt to identify potential cross-colony correlates of sparrow abundance we recorded a  
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18 suite of habitat and environmental variables across all 66 study sites (described in Table 1). As  
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20 potential correlates of sparrow reproductive success we mapped the total area of domestic  
21  
22 gardens (GARDE) and green space (parks, amenity grassland and roadside grass verges;  
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24 GREEN) within core survey areas plus a 50 m surrounding buffer. Within core areas only we  
25  
26 also mapped the extent of three fine-scale habitat features known to be frequently utilised by  
27  
28 foraging sparrows during the breeding season in suburban areas (Vincent 2006). An index of  
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30 woody vegetation volume (WOODY) was derived by summing categorical scores for scrub  
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32 (height x width categories where <2 m=1, 2-5 m=3, >5 m=5, within 5 m sections of hedge or  
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34 garden border), trees (>5 m tall; small=5, medium=7.5, large=10) and patches of bramble *Rubus*  
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36 spp. or *Buddleia* spp. (<20 m<sup>2</sup> = 20, 20-100 m<sup>2</sup>=60, >100 m<sup>2</sup>=100). Areas of potentially weed-  
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38 rich (wasteland, brownfield, allotments, tilled ground; SEEDY) and insect-rich habitats  
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40 (grassland and ruderal vegetation; GRASS) were also mapped. We measured the density of  
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42 residential buildings (HOUSE) within core survey areas using 2007 satellite images (Google  
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44 Earth, Google Inc, USA) after excluding any green or brown space.  
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55 Habitat character at the wider core plus 200 m scale was described using the remotely sensed  
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57 CEH Land Cover Map (LCM) from 2000 (Fuller et al. 2002). Seventeen LCM habitat categories  
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4 were combined into five aggregate categories (woodland, grassland, disturbed land, wetland and  
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6 urban) which were subject to a principal components analysis. The first principal component  
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8 (PCA1) explained 38% of the variation and provided a measure of managed non-urban land  
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10 (being negatively correlated with urban area ( $r=-0.67$ ) and positively correlated with the extent of  
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12 grassland (0.58) and disturbed land (0.42)). The second axis (PCA2) accounted for a further 21%  
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14 of the variation and reflected the local extent of wetland (0.72) and woodland (0.58).  
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21 Environmental variables included the level of background supplementary feeding (BFEED) and  
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23 the density of domestic cats (CAT) both estimated from surveys of local residents. At each  
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25 colony we attempted to conduct face-to-face questionnaire interviews at every property within  
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27 the core survey area. If the residents were out, a questionnaire was posted with a return address.  
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29 Of the 1750 completed questionnaires, 80% were completed face-to-face, with a mean of 26.5  
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31 returns per colony (range 16-46), equivalent to 51% of all households (range 22-94%). Residents  
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33 were asked how many cats they owned and details of the type and frequency of any  
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35 supplementary food provision. We adopted the method of Baker et al. (2008) to allow for  
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37 differential cat reporting rates between face-to-face and postal returns (see Peach et al. (2013) for  
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39 details). To provide an index of background supplementary feeding we multiplied a measure of  
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41 the scale of provision (score for each large feeder or bird table=2; small feeder, fatballs or  
42  
43 bread=1) by the frequency of provision (1=continuous provision; 0.75=food available on more  
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45 than 50% of days; 0.5=food available on less than 50% of days) at each household. We then  
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47 multiplied the mean of these household scores by the number of households within the core  
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49 survey area. A relative measure of local Sparrowhawk activity (HAWK) was provided by the  
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4 proportion of all sparrow surveys conducted during 2006-2009 (n=17) on which at least one  
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6 Sparrowhawk was recorded.  
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11 Ground level nitrogen dioxide (NO<sub>2</sub>) measures were derived from a kernel-based pollution  
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13 dispersion model (King College's Air Pollution Toolkit) which combines point measures, traffic  
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15 flows and emissions with hourly meteorological data to predict air pollution levels at a 20 m-grid  
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17 resolution across London (Tonne et al. 2008). The model predicts average annual NO<sub>2</sub> levels at  
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19 this scale with a high level of accuracy ( $R^2 = 0.76$ , root mean square error = 14%) and outputs  
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21 from a similar dispersion model predict variation in lichen diversity on individual trees across  
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23 London (Davies et al. 2007). We used predicted annual mean NO<sub>2</sub> levels for a single (typical)  
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25 calendar year (2004) averaged across all grid points within core survey areas (mean =30.7 points  
26  
27 per study site), a measure that was strongly correlated (across study sites) with an identical  
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29 measure for 2003 ( $r=0.98$ ,  $P<0.0001$ ) and a similar predicted measure of small particulate matter  
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31 for 2004 ( $r=0.94$ ,  $P<0.0001$ ). Electromagnetic radiation (EMR) was measured at each colony  
32  
33 between 11:00 and 14:00 on week days (Monday to Friday) during June-July 2008. Maximum  
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35 (peak hold) electric field strength (V/m) over a 2-minute period was recorded at 50-m intervals  
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37 along the entire fledgling transect route (mean 23.4 readings per site, range 16-33).  
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45 Measurements were based on the downlink frequencies of GSM 900 / 1800 MHz (925-960 MHz,  
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47 1805-1880 MHz) using a calibrated high-frequency spectrum analyser (ROM Elektronik RF  
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49 survey meter, model HFR-4 s/n 262808) with calibrated EMC directional antenna which was  
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51 rotated around 360-degrees to ensure a maximum measure. Finally we used published indices of  
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53 social deprivation (Noble et al. 2006) to test whether sparrows were more abundant in socially  
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55 deprived localities (as proposed by Shaw et al. (2008)). For each colony we calculated a mean  
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4 rank index of multiple deprivation for 2007 weighted by the area of each lower super output area  
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6 (the scale at which deprivation is measured) within each core plus 50 m buffer (SODEP).  
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## 10 11 **Statistical analysis** 12 13

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15 We used generalised linear mixed models (GLMMs) with Poisson distributions to test whether  
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17 supplementary feeding influenced the abundance of fledglings or territorial male House  
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19 Sparrows. COLONY was declared as a random term, and where necessary COLONY\*YEAR to  
20  
21 deal with over-dispersion. The fledgling GLMM took the annual aggregate core count of  
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23 fledglings as the dependent variable, and specified the natural logarithm of  $MCM_c$  as an offset  
24  
25 term to provide a *per capita* measure of fledgling abundance. Two nuisance variables were  
26  
27 included as fixed effects: OBSERVER (5-level factor) and the proportion of  $MCM_{cb}$  counts in  
28  
29 the 200 m buffer ( $MCM_b/MCM_{cb}$  or 'PBUFF') to allow for fledglings originating from nests in  
30  
31 the 200 m buffer being recorded in the core area following local dispersal (Peach et al. 2015).  
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33 Initially we tested for an effect of supplementary feeding on fledgling counts by including the  
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35 terms FED (fed, unfed), YEAR (4-level factor: 2005-08) and colony SIZE (small, medium,  
36  
37 large) and all possible interactions. In order to test whether any effect of supplementary feeding  
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39 on fledgling abundance changed following the introduction of seed in May 2007, the term YEAR  
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41 was replaced by the term PERIOD (before/after the introduction of seed), and the interaction  
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43 FED\*PERIOD tested for a change in any response to feeding following the introduction of seed  
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45 (after the removal of a non-significant SIZE\*FED interaction).  
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56 We tested for effects of supplementary feeding on counts of territorial males at the core plus 200  
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58 m scale using a GLMM in which  $MCM_{cb}$  was the dependent variable, COLONY was a random  
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4 term, and OBSERVER, YEAR, feeding treatment (FED) and density of territorial males (DEN)  
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6 in the first survey year were fixed effects, with all interactions involving YEAR, FED and DEN.  
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8 A different analytical approach was required to test for any additive effect of seed provision on  
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10 MCM<sub>cb</sub> counts in 2008 and 2009. For this we included fixed effects for OBSERVER, YEAR,  
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12 FED and FED\*DEN to allow for a density-dependent effect of mealworm provision on MCM<sub>cb</sub>  
13  
14 (Peach et al. 2015). To test for an additive effect of seed provision, we included a two-level  
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16 factor (SEED) that was coded '0' for all colonies during 2005-2007, and '1' for all fed colonies  
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18 during 2008 and 2009. We checked whether any effect of experimental seed provision was  
19  
20 modified by the level of background supplementary feeding measured at each colony by adding a  
21  
22 three-level factor (BFEEDC) factor reflecting high, medium and low levels of background  
23  
24 feeding by residents (three equal divisions of BFEED), and its interaction with SEED. Finally,  
25  
26 we tested whether changes in MCM<sub>cb</sub> were related to the observed seed consumption rate (high,  
27  
28 medium, low: SEEDC) with and without the BFEEDC term allowing for variation in background  
29  
30 feeding across study colonies. Seed consumption rate at each colony was estimated by  
31  
32 multiplying total seed provision over the 23 month feeding period by the proportion of 15-minute  
33  
34 feeder watches (total number of watches=2885, range=13-473 per colony) during which house  
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36 sparrows were observed feeding on our sunflower hearts (mean=0.783, range=0.299-1.000).  
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48 We tested for relationships between habitat / environmental variables and cross-colony variation  
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50 in (i) *per capita* fledgling abundance, (ii) the density of territorial males before the introduction  
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52 of our supplementary feeding, and (iii) linear temporal trends in counts of territorial males  
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54 between 2005 and 2009. Fledgling abundance was measured at the core colony scale, and  
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56 involved screening variables recorded mainly at the same or slightly coarser scale of core plus 50  
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4 m (Table 1). Adult male abundance was analysed at the core plus 200 m scale, and involved  
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6 screening variables measured at the core and wider scales (Table 1). Over the 5 years of surveys,  
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8 27% of all recorded territorial males were located within core survey areas, the rest in the 200m  
9  
10 buffer. In each analysis we started with a base model that included all important terms associated  
11  
12 with study design and supplementary feeding, and in a first step screened a set of habitat  
13  
14 variables to identify any important predictors of sparrow abundance. In a second step we  
15  
16 screened a set of environmental variables (urban stressors) that might plausibly have limited  
17  
18 sparrow abundance. At each step, all candidate variables were added to the base model and  
19  
20 backwards deletion was used to remove the least significant predictors of sparrow abundance  
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22 one-by-one. Any significant habitat predictors identified in step one were retained in step two  
23  
24 irrespective of any changes in statistical significance to ensure any relationships involving urban  
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26 stressors were robust to any underlying habitat effects. Correlations between habitat and  
27  
28 environmental variables were generally weak with only five out of 91 exceeding 0.4, and 3  
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30 exceeding 0.5 (Online Resource 1, Table A1). Stepwise deletion has been shown to perform as  
31  
32 well as other model selection methods including information theoretic approaches (Murtaugh  
33  
34 2009) and gave us the flexibility to retain non-significant terms (e.g. relating to study design or  
35  
36 habitat) and to test for interactions (see below).  
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48 The base GLMM for fledgling abundance included the terms OBS, PBUFF, YEAR, SIZE, FED  
49  
50 and YEAR\*SIZE, as well as random COLONY and COLONY\*YEAR terms. As our feeding  
51  
52 treatment affected fledgling abundance (see Results), we checked all significant predictors for  
53  
54 interactions with FED. Generalised linear models (GLMs) were used to analyse cross-colony  
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56 variation in male sparrow abundance. The dependent variable for male density was the observed  
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4 count of territorial males at the core + 200 m scale ( $MCM_{cb}$ ) before supplementary feeding began  
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6 (in either 2005 or 2006) corrected for the effects of observer (taken from the GLMM of adult  
7  
8 abundance, above), divided by the survey area, and declaring a Normal error structure (no other  
9  
10 design variables were needed). The base GLM testing for correlates of temporal trends in male  
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12 abundance included the fixed effects OBS, COLONY and YEAR (defined as a linear covariate)  
13  
14 plus an interaction between sparrow density (DEN) and year to allow for a density-dependent  
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16 pattern of temporal change in colony size (Peach et al. 2015). Cross-colony correlates of trend in  
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18 male abundance were tested through the addition of interaction terms between year and each  
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20 habitat/environmental variable ( $YEAR*VAR$ ), checking in each case for any modifying effect of  
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22 local population density ( $YEAR*VAR*DEN$ ).  
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31 GLMs and GLMMs were fitted using the GENMOD and GLIMMIX procedures of SAS version  
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33 9.4 (SAS Institute, Cary, NC, USA) using Wald tests to assess the significance of fixed effects  
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35 and (for GLMMs) the Satterthwaite method for calculating degrees of freedom. Final models  
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37 were checked for evidence of residual heteroscedasticity and influential observations.  
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43 We estimated monthly survival from our resighting data by fitting Cormack-Jolly-Seber (CJS)  
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45 models which describe the encounter histories as the product of resighting and apparent survival  
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47 probabilities (Lebreton et al. 1992). The data from the two winters were analysed separately. The  
48  
49 main aim of the analysis was to test for an effect of supplementary feeding on survival but in  
50  
51 order to maximise statistical power we first identified plausible and parsimonious model  
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53 descriptions of the encounter history data. First we checked the assumptions of the CJS model by  
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55 running goodness-of fit tests from program RELEASE (Lebreton et al. 1992) on encounter  
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4 history data for males and females from five sites in 2007-08 and four sites in 2008-09. There  
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6 was no evidence of trap-dependence (RELEASE Test 2:  $\chi^2_{31} = 25.2$ ,  $P > 0.75$  for 2007-08 &  $\chi^2_{20} =$   
7  
8 10.4,  $P > 0.95$  for 2008-09) but some evidence for an excess of transient individuals in some  
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10 groups (significant test 3.SR for 4 out of 10 groups in 2007-08, and 2 out of 8 groups in 2008-09;  
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12 Online Resource 1, Table A2). We dealt with transients by imposing an age structure in which  
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14 survival during the first month after initial capture differed from that during all subsequent  
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16 months (Williams et al. 2001). We also tested for additive and multiplicative effects of sex and  
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18 site on survival, and of sex, site and time period (month) on recapture probability. In order to  
19  
20 maximise statistical power to detect any effect of supplementary feeding, we did not consider  
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22 temporal (monthly) variation in survival. Once a relatively parsimonious (low AIC) description  
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24 of survival and resighting had been achieved, we added supplementary feeding to the model as  
25  
26 an additive individual covariate (Williams et al. 2001) which tested whether apparent survival  
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28 differed between fed and unfed sites. Although our approach potentially confounds  
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30 supplementary feeding and any underlying site effects, the wider experimental design required  
31  
32 the feeding treatment to be maintained across years. Fed and unfed study sites shared generally  
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34 similar habitat and environmental characteristics especially for key traits like the extent of seed-  
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36 rich habitat and background supplementary feeding (Online Resource 1, Table A3).  
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## 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 (Fig. 2). The net impact of

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4 feeding amounted to an increase in male abundance at fed colonies of just 3.3% (based on  
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6 predicted aggregate counts in 2005 and 2009 of 731.8 and 645.2 respectively at unfed colonies,  
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8 and 773.5 and 705.0 at fed colonies, equivalent to 23 additional territorial males across the 33  
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10 fed colonies).  
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16 After allowing for the density-dependent effect of supplementary feeding on male abundance,  
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18 there was no evidence of any additive effect of year-round seed provision (Table 4). This was  
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20 true when seed provision was defined as a two-level factor (model A, Table 4), and as a three-  
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22 level seed consumption rate (model C), and after allowing for cross-colony variation in the  
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24 extent of background feeding (models B & D, Table 4).  
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### 31 **Correlates of cross-colony variation in sparrow abundance**

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36 Our study colonies exhibited wide variation in habitat character, housing density, background  
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38 supplementary feeding, domestic cat density, air pollution and human social deprivation (Table  
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40 1). *Per capita* fledgling counts declined as garden area and Sparrowhawk activity increased  
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42 (Table 5, Fig. 3). Area of seed-rich habitat was positively related to fledgling counts at unfed  
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44 colonies ( $t_{55}=2.19$ ,  $P=0.033$ ) with a weaker negative relationship ( $t_{52}=-1.90$ ,  $P=0.063$ ) at fed  
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46 colonies (Fig. 3), the interaction being highly significant (Table 5).  
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53 Prior to the initiation of supplementary feeding, the density of territorial male sparrows was  
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55 positively related to PCA1 (the extent of disturbed land and grassland) although this relationship  
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57 was rendered non-significant by the inclusion of a strong negative relationship involving  
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4 nitrogen dioxide air pollution (Table 5, Fig. 4). Temporal trends in male abundance varied  
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6 significantly between colony density categories (YEAR\*DEN:  $F_{2,244} = 24.3$ ,  $P < 0.0001$ ),  
7  
8 declining significantly at high density colonies but showing no overall trends at low and medium  
9  
10 density colonies (Fig. 2). Both significant correlates of cross-colony variation in trends in male  
11  
12 abundance exhibited density-dependence (Table 5). Trends in abundance at high density colonies  
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14 were positively related to the area of seed-rich habitat, while trends at medium-density colonies  
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16 were negatively related to nitrogen dioxide air pollution (Fig. 5).  
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## 23 **Discussion**

### 24 **Effects of food supplementation**

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33 Our previous studies documented positive effects of mealworm supplementation on House  
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35 Sparrow nesting success (+55%; Peach et al. (2014)), fledgling abundance (+62%) and adult  
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37 male abundance in low density colonies (+36% following two seasons of feeding; Peach et al.  
38  
39 (2015)). Similar impacts were evident over the four years of supplementary feeding considered  
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41 here (fledgling abundance: +55%; adult male abundance at low density colonies: +33%) and  
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43 there was no evidence of any additive effect of unlimited year-round seed provision during the  
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45 third and fourth year of supplementary feeding. Given the similar magnitudes of feeding impacts  
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47 on sparrow abundance before and after the introduction of seed, and the absence of any effect of  
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49 feeding on overwinter survival, we conclude that the addition of unlimited seed to the  
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51 experimental feeding treatment had no impact on sparrow demography or abundance. The large  
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53 positive effect of mealworm supplementation on fledgling counts probably reflects a widespread  
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4 limiting effect of invertebrate availability on House Sparrow reproductive success and chick  
5 condition in urban environments (Peach et al. 2008; Seress et al. 2012; Peach et al. 2015).  
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11 Our results clearly indicate that despite invertebrate availability limiting reproductive success,  
12 food availability more broadly (encompassing breeding season invertebrate availability and year  
13 round seed availability) does not limit the size of the suburban House Sparrow population across  
14 London. Had food availability limited the survival of young sparrows between the post-fledging  
15 period (July) and recruitment as first-time breeders (March-April), or the survival of adults, we  
16 would have expected to measure higher overwinter survival and increased abundance of  
17 territorial male sparrows at fed colonies. This is particularly true given the depleted status of our  
18 wider study population and the low rates of natal dispersal in House Sparrows particularly in  
19 suburban landscapes (i.e. any demographic impacts should have been evident locally; Fleischer  
20 et al. 1984; Paradis et al. 1998; Vangestel et al. 2011). Our conclusion that food availability  
21 limits the development and survival of urban House Sparrow chicks but not fully grown birds  
22 (after July of the first summer of life) is consistent with the age related impacts of urbanisation  
23 reported for sparrow tarsus length and feather quality (Meillere et al. 2017). The absence of any  
24 post-fledging demographic response to our experimental food provision implies that factors  
25 unrelated to food availability probably drove the recent population decline affecting London  
26 House Sparrows.  
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53 It is important to acknowledge that background supplementary feeding was ubiquitous (albeit  
54 highly variable) across our 66 study sites (Table 1). Our study compared substantial breeding  
55 season protein supplementation (estimated to have satisfied 82% of local chick energy  
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4 requirements; Peach et al. 2015) plus unlimited year-round high energy seed provision against  
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6 current levels of background food provision (mainly seed, fat balls and other vegetable materials;  
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8 protein supplementation was rare). It may be that current levels of background food provision are  
9  
10 sufficient to avoid demographic limitation linked to food availability, but this does not affect our  
11  
12 conclusion that food availability is unlikely to have caused the recent House Sparrow population  
13  
14 decline across London. It is also unlikely that unusual weather conditions during our study  
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16 might have negated or offset any potential impacts of supplementary feeding on sparrows. Of the  
17  
18 four study summers, two were relatively wet (2007 & 2008) and one relatively dry (2005), and of  
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20 the two fed winters, one was relatively mild (2007-08) and the other relatively cold (2008-09)  
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22 (Online Resource 1, Table A6).  
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### 31 **Correlates of sparrow abundance**

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36 Despite marked variation in habitat character across the 66 study colonies, our analysis identified  
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38 only one habitat (seed-rich) as having a potential influence on House Sparrow abundance.  
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40 Relatively high fledgling counts in unfed survey areas having large areas of wasteland, disturbed  
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42 land or allotments could reflect greater usage of these seed-rich habitats at colonies lacking our  
43  
44 supplementary feeding or perhaps higher detectability of young sparrows in these relatively  
45  
46 accessible open habitats. However, the positive relationship between the extent of seed-rich  
47  
48 habitat and the temporal trend in adult male abundance is more likely to reflect a genuine impact  
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50 of seed-rich habitat on sparrow demography as sparrows are largely granivorous outside of the  
51  
52 breeding season, and are known to select seed-rich and disturbed habitats for foraging (Mitschke  
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54 et al. 2000; Anderson 2006; Chamberlain et al. 2007). The restriction of this relationship to high  
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4 density sparrow sites might reflect a tendency for seed-rich habitat to limit sparrow demography  
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6 only in localities where there may be competition for the associated seed resources. Although  
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8 garden area had a negative influence on fledgling counts this relationship might simply reflect a  
9  
10 tendency for fledglings to be under-recorded in survey areas having a high cover of privately-  
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12 owned domestic gardens to which our surveyors will have had only partial access.  
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19 The negative relationship between Sparrowhawk activity and fledgling abundance could reflect  
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21 genuinely lower abundance (perhaps linked to increased predation mortality) or a behavioural  
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23 response of sparrows to hawk activity. Both of these interpretations also apply to a study  
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25 reporting negative correlations between sparrow counts and hawk activity in UK gardens (Bell et  
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27 al. 2010). Adult male density was positively related to hawk activity although this relationship  
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29 disappeared when other stronger predictors of male density were included in GLMs (Table 4).  
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33 Our measure of hawk activity was relatively crude and may not reliably reflect true cross-colony  
34  
35 variation in Sparrowhawk hunting activity. All three of our sparrow density measures were  
36  
37 unrelated to the density of domestic cats despite wide cross-colony variation in the latter (0.0-  
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39 25.9 cats ha<sup>-1</sup>). Previous studies have reported rates of cat depredation on rural and suburban  
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41 House Sparrow populations high enough to potentially limit population size (Churcher and  
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43 Lawton 1987; Thomas et al. 2012).  
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51 The relationship between the density of territorial male sparrows and local nitrogen dioxide air  
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53 pollution was statistically strong and robust to any confounding effects of habitat or other  
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55 potential environmental stressors (Table 4, Fig. 4). Most of the recent decline in House Sparrow  
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57 abundance across London occurred prior to the commencement of this study (1995-2005: 60%  
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4 decline; 1995-2015: 71% decline; unpublished Breeding Bird Survey data), so any distribution or  
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6 abundance patterns relating to environmental drivers of population change should have been  
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8 apparent by the start of our study in 2005. Our data also indicate more negative temporal trends  
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10 in territorial male abundance at colonies subjected to higher levels of air pollution albeit  
11  
12 restricted to colonies of intermediate initial density (Fig. 5). Anthropogenic air pollutants like  
13  
14 nitrogen dioxide and trace metals are known to have a variety of impacts on the physiology and  
15  
16 health status of a wide range of vertebrates including birds, mammals and humans (Isaksson  
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18 2010; Koivula and Eeva, 2010). Prolonged exposure to air pollutants can cause oxidative stress  
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20 and inflammation leading to tissue damage linked to disease and senescence (Isaksson 2015).  
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22 Oxidative stress is negatively associated with several avian fitness traits including immune  
23  
24 response, reproduction and survival (Costantini 2008). House Sparrows from more urbanised  
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26 localities have higher physiological indicators of oxidative stress (haemoglobin and total  
27  
28 antioxidant capacity) than their rural counterparts (Herrera-Duenas et al. 2014), and higher levels  
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30 of lead in feathers was associated with a higher prevalence of avian malaria *Plasmodium*  
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32 *relictum* (Bichet et al. 2013). Furthermore, House Sparrow nests in localities with higher levels  
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34 of air pollution contained chicks in poorer condition and with smaller tarsi (Peach et al. 2008).  
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36 The correlations reported here between air pollution and sparrow breeding density, and trends in  
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38 breeding density, suggest some component (or correlate) of air pollution may be affecting the  
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40 fitness of this species in urban landscapes and thereby contributing to ongoing population  
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42 declines.  
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## Conclusions



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4 This study conclusively demonstrates that food availability is not limiting an extensive declining  
5 suburban sparrow population. Increasing food availability is unlikely on its own to lead to any  
6 recovery of the London sparrow population. However, the availability of invertebrate prey limits  
7 reproductive success and chick development in urban House Sparrows and management to  
8 increase invertebrate availability may therefore be beneficial as part of a wider package of  
9 conservation measures. This study supports previous work in providing evidence for the benefits  
10 to sparrows of seed-rich habitats like allotments and disturbed land (Chamberlain et al. 2007)  
11 and such habitats should be maintained and provided where absent. Finally, this study provides  
12 correlative evidence of negative impacts of air pollution on sparrow abundance, and given the  
13 growing concerns about air pollution impacts on human health in many modern cities, this issue  
14 merits further investigation.  
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58 Birds.  
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**Table 1** Potential covariates of house sparrow abundance measured at each of the 66 breeding colonies in Greater London. 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 + 50m 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.

Category	Label	Description	Scale measured	Year(s)	Median (Range)
Habitat	GARDE	% cover domestic garden	Core + 50m	2007	38 (1 – 66)
Habitat	GREEN	% cover open green space (amenity grass, parks, grass verges)	Core + 50m	2007	5 (0 – 40)
Habitat	PCA1	1 <sup>st</sup> PCA axis of LCM2000 (reflects extent of grassland & disturbed land)	Core + 200m	2000	-0.55 (-1.27 – 6.21)
Habitat	PCA2	2 <sup>nd</sup> PCA axis of LCM2000 (reflects extent of wetland & woodland)	Core + 200m	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 + 200m	2006-09	2 (0 – 7)
Pollutant	NO2	Nitrogen dioxide concentration (dispersion model; $\mu\text{g m}^{-3}$ )	Core	2004	35.2 (29.6 – 47.2)
Pollutant	EMR	Median electromagnetic radiation score (V/m)	Core + 50m	2008	69.5 (21 – 675)
Socio-econ	SODEP	Socio-economic deprivation index (weighted mean rank; low=deprived)	Core + 50m	2007	13,814 (2,655– 30,480)

**Table 2** Testing for an effect of supplementary feeding on *per capita* fledgling abundance during 2005-08. 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<sub>c</sub>) as offset terms. Fixed effects were observer, proportion of MCM in the 200 m buffer (PBUFF), year, colony size (small, medium, large: SIZE<sub>cb</sub>), feeding treatment (FED, unfed) and period without (2005/6) and with (2007/8) seed provision (PERIOD). Random terms were colony and colony\*year.

Model terms	<i>P</i> 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	

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

Model terms	<i>P</i> 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 4** Testing for an additive effect of seed provision on the abundance of territorial male sparrows ( $MCM_{cb}$ ). 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 sparrow density (low, medium, high). 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 term 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

Model terms	(A) Base + Seed Provision <sup>1</sup>	(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 <sup>2</sup>	0.159 <sup>2</sup>
BFEEDC	-	0.130	-	0.264
BFEEDC*SEED/SEEDC	-	0.704	-	0.185 <sup>2</sup>

1. 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 ( $P>0.18$ ).

2. These *P* values relate to the term SEEDC.

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

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
<i>Habitats</i>										
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
<i>Environmental</i>										
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	-	
<i>Final models:</i>										
<i>Model terms</i>	<i>P-value</i>			<i>Model terms</i>	<i>P-value</i>			<i>Model terms</i>	<i>P-value</i>	
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									

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4 **Figure Captions**  
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9 **Fig. 1** Monthly overwinter survival rates ( $\pm$  SE) of male house sparrows at fed (filled bars) and  
10 unfed (open bars) colonies during the winters 2007-08 and 2008-09. Colonies A-D were  
11 supplementary fed with mealworms and year-round sunflower hearts, while colonies E-F were  
12 not. Survival estimates are taken from the most parsimonious models including site-specific  
13 survival parameters (Table A4).  
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23 **Fig. 2** Mean maximum counts of chirping males during 2005-09 within core-plus-200m buffer  
24 areas in colonies of low (a), medium (b) and high (c) initial density. Bars show predicted means  
25 ( $\pm$  SE) and square symbols show raw mean counts. Filled bars/symbols indicate fed colonies  
26 and open bars/symbols unfed colonies. \* Statistically significant ( $P < 0.05$ ) post-hoc differences  
27 between predicted means at fed and unfed colonies.  
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38 **Fig. 3** Relationships between per capita fledgling abundance and (a) the proportional cover of  
39 domestic gardens, (b) Sparrowhawk activity and (c) the area of seed-rich habitats at fed (filled  
40 symbols) and unfed (open symbols) colonies. See Methods for variable definitions.  
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48 **Fig. 4** Relationship between the density of territorial male sparrows and average year-round  
49 nitrogen dioxide concentration in the air. See Methods for nitrogen dioxide derivation.  
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55 **Fig. 5** Relationships between the linear trend in male abundance during 2005-09 and (a) average  
56 year-round nitrogen dioxide concentration at medium density colonies (open squares) and (b) the  
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area of seed-rich habitats at high density colonies (filled squares). Open circles indicate low density colonies. See Methods for variable definitions.



Fig.1

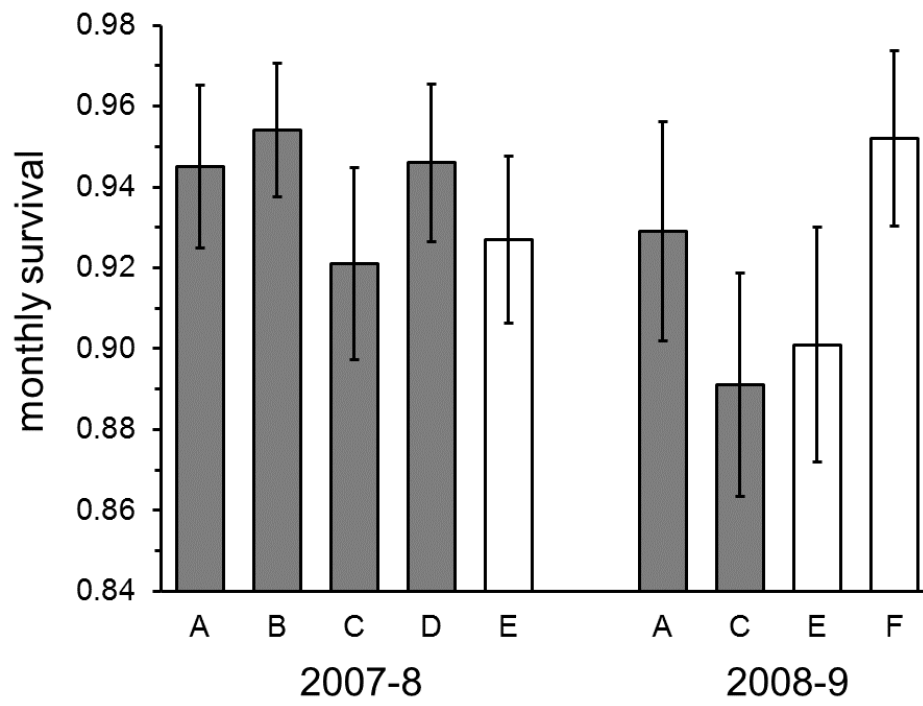


Fig. 2

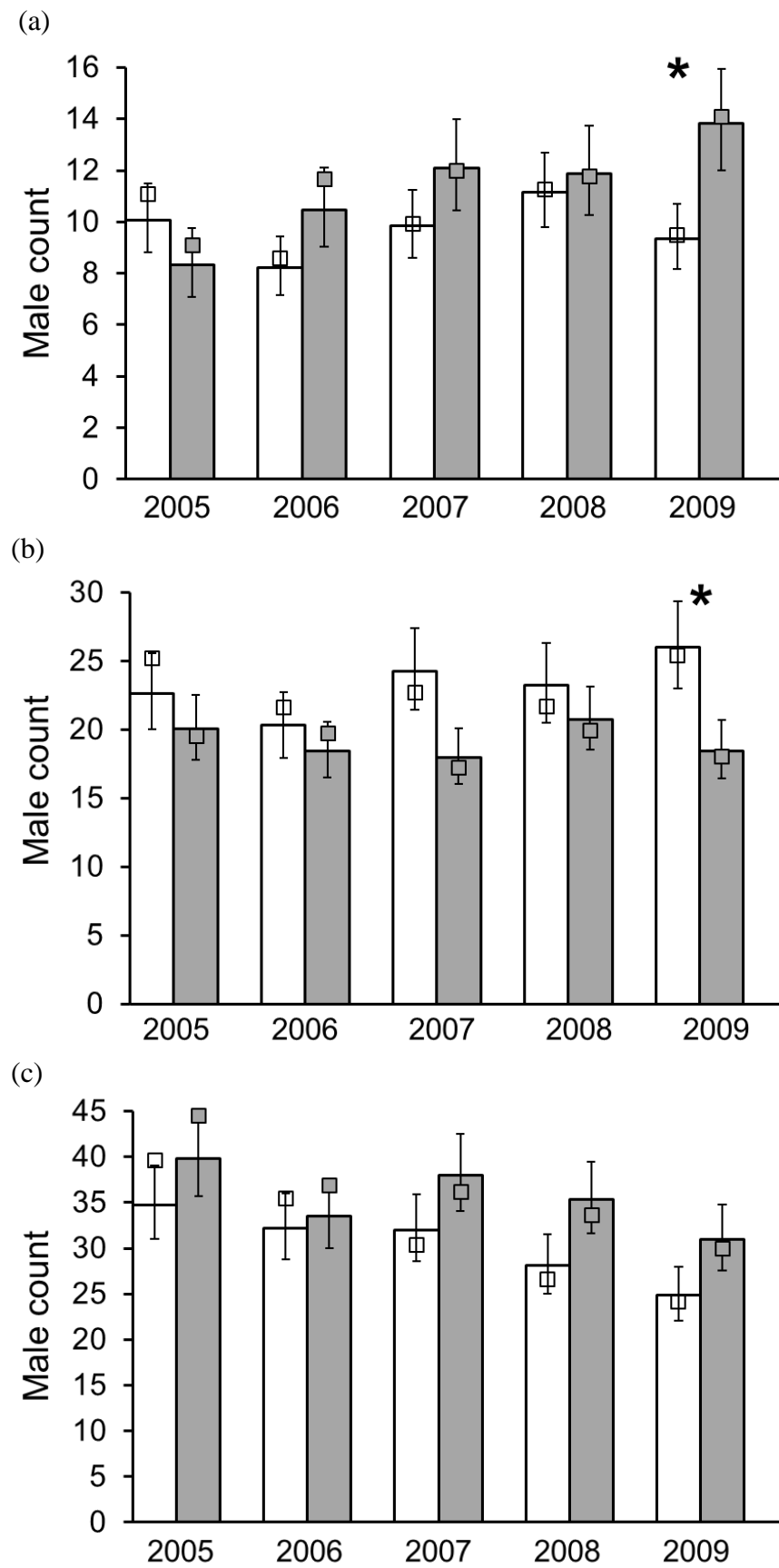


Fig 3

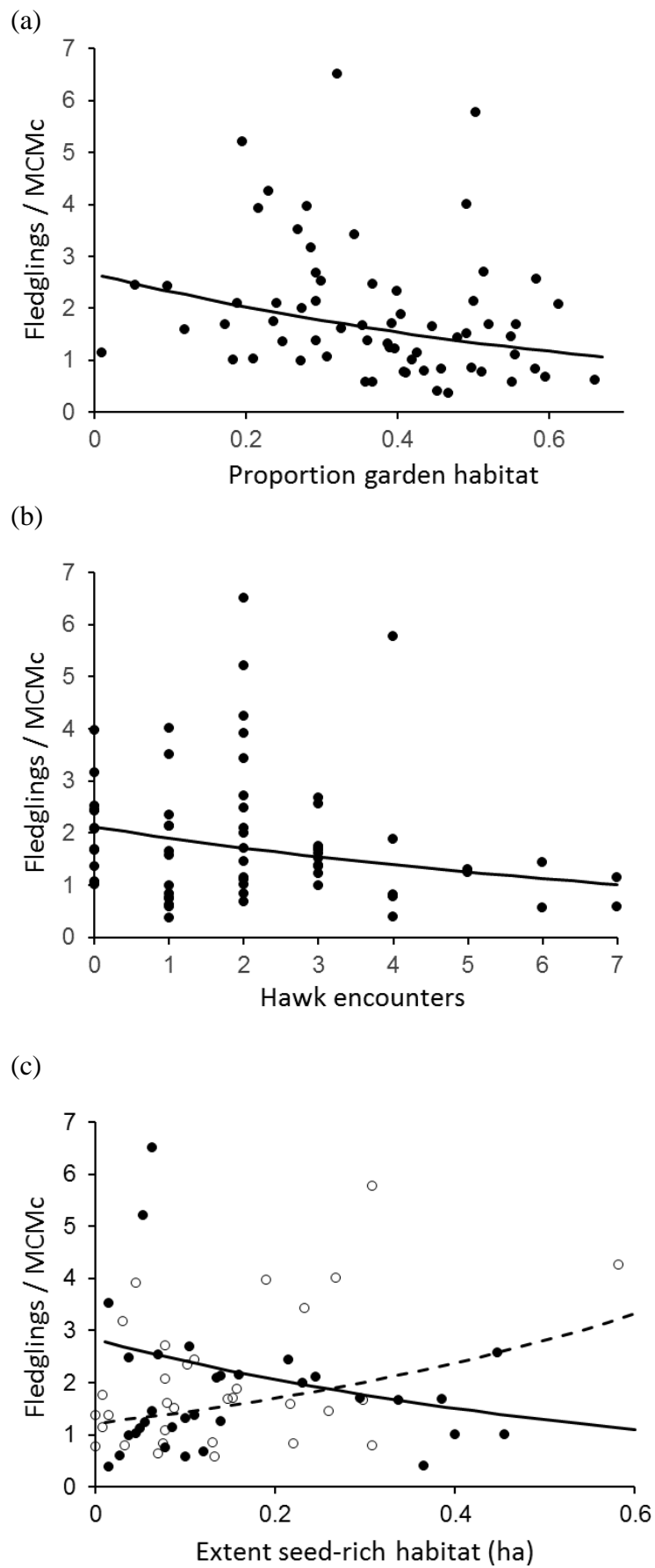


Fig 4

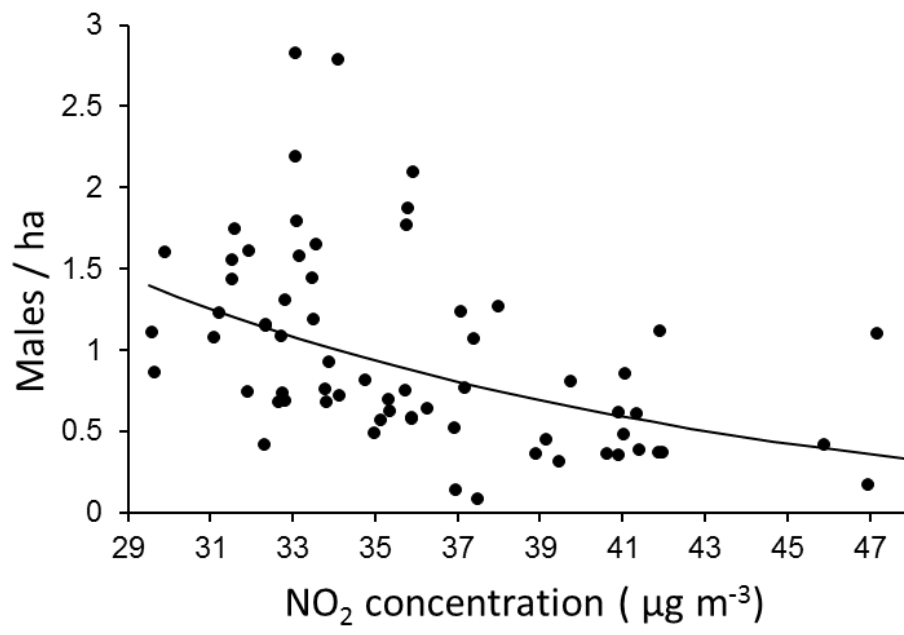
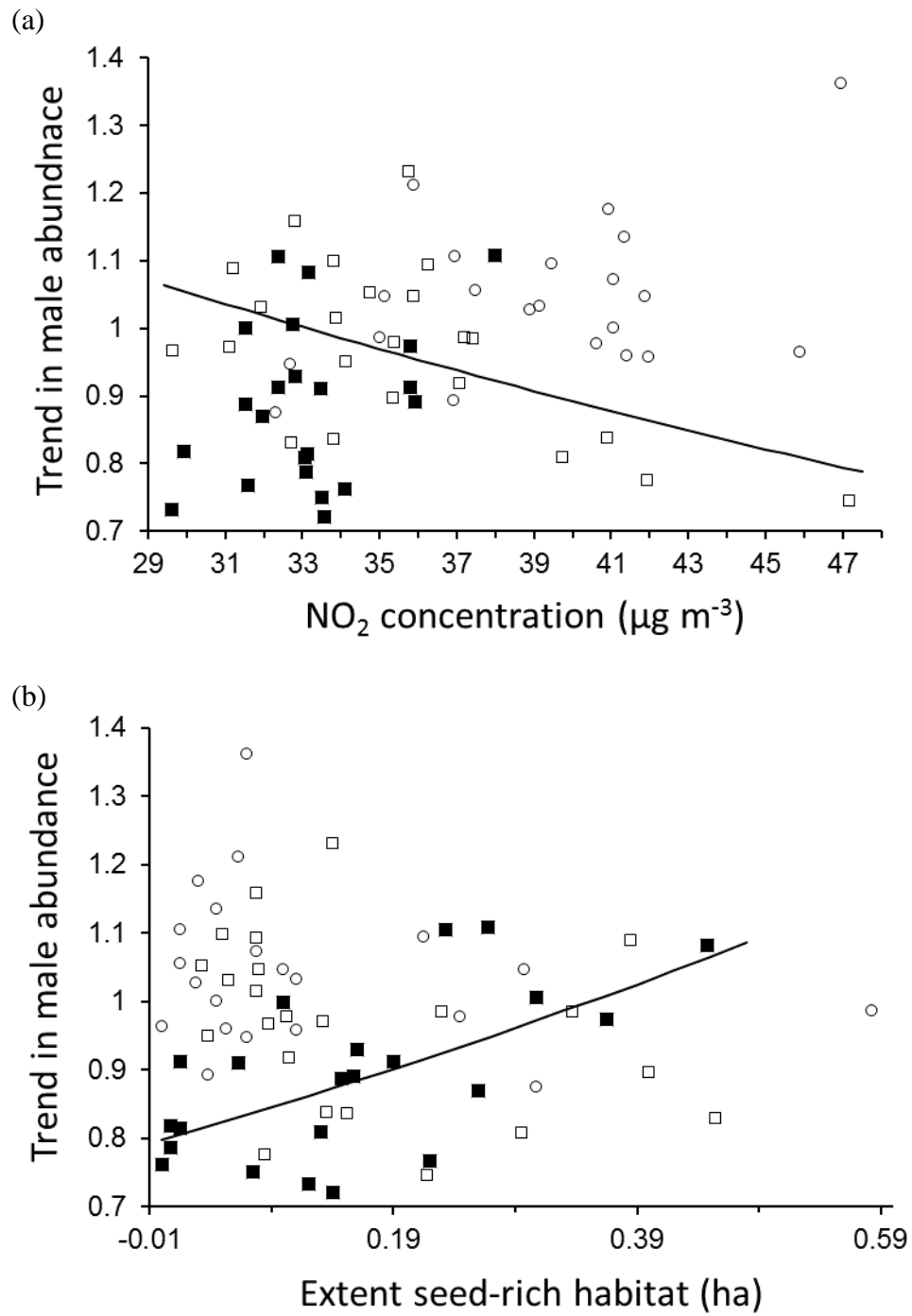


Fig 5



Authors Responses to referees (in red):

Reviewer #1: The range of data considered in this paper is impressive, and the conclusions seem well balanced. In a complex environment, it will always be challenging to move from correlation to identifying causative factors. My own limited experience of some (southern hemisphere) House Sparrow populations is that they tend to be very localised in urban environments, often absent from suburbs with gardens and trees and concentrated in commercial areas; particularly associated with supermarkets. Yet there are many isolated populations along main routes, at petrol stations with shops and restaurants attached.

The writing is clear and correct to my ear, and the referencing commendably accurate. Three small corrections needed:

Introduction, line 12: Chace (as here) or Chase (as in references)? **Typo corrected.**

Conclusions, line 43 "to recover the London sparrow population" reads oddly; "restore", or a different formulation, would be better. **Sentence reworded at page 24, lines 2-3 : Increasing food availability is unlikely on its own to lead to any recovery of the London sparrow population.**

References, page 28 top: "Jones & Reynolds 2008" is out of alphabetical order, and should follow "Isaksson & Andersson 2007". **Reference order corrected.**

Reviewer #2:

### **Specific comments:**

#### **Introduction**

Page 4 Line 21: change 'has' to 'have' . **Typo corrected.**

Page 5 line 19: Without knowing the details of the study referenced, is it not possible that any population effects of the supplementary feeding would take a few generations to become apparent? i.e. has feeding persisted for several generations with consistent surveys to confirm this? **The cited study was conducted over 3 years (2 fed generations), which can obviously be checked by any reader. The full study reported in the current study spanned 5 years (4 fed generations) and so we would therefore expect even delayed effects of feeding to be evident in bird surveys by years 4 or 5 of the study. No similar comments made in methods about full study duration so we assume the referee is happy with the 5 year study period. No changes made to text.**

Page 5 Line 46: Do the authors mean single species demography? Studies on bird demography and abundance in response to urban feeders are available. Perhaps this sentence should be clarified. **We have checked the literature and virtually all demographic studies (i.e. measuring demographic rates or changes in abundance in time or space) of supplementary feeding of birds have been conducted in rural habitats (probably because it is difficult to manipulate food supply in urban landscapes). We make this point and cite two example references at page 5, lines 19-22.**

Page 6 line 47: perhaps re-word here, as this sentence suggests no micronutrients or natural foraging are required/performed by the birds. I.e. In addition to natural foraging supplementary feeding of..... **Sentence reworded as suggested at page 7, lines 1-4.**

#### **Methods**

Was the seed or mealworms in feeders ever finished? Sentence added to explain this at page 6, lines 22 to page 7, line 1.

Page 7 line 12: How were these percentages calculated? If they are referring to the same thing should they not add up to 100% or less (in the case of unaccounted species)? The % figures show the proportion of feeder watches during which each species was recorded (frequency of occurrence). Text revised to clarify this at page 7, lines 10-11.

### General

Of interest is the fact that this species is declining in mostly native areas, yet is a successful invader elsewhere. In these invaded countries are these populations expanding? Can the authors comment on any factors which may benefit these species in invaded areas, but are absent in their native areas? We don't have data either on population changes in invaded countries or on factors that benefit this species in invaded areas, so we cannot usefully comment. No change made to text.

Linked to this, has the expanding population of parakeets not potentially affected Sparrows in terms of competition at feeders (for which references are available on the importance especially in winter) and cavity nests? Were these recorded at any of your feeders? House sparrows only rarely nest in cavities so are unlikely to compete with Ring-necked parakeets (RP) for nest sites. RPs were recorded at our seed feeders on only 5.5% of feeder watches and at only 8 of the 33 supplementary fed sites. RP's still have a limited distribution across London mainly confined to northern and western districts. Usage of our seed feeders by sparrows was generally high across sites with sparrows being recorded on average during 78% of feeder watches (range across sites: 30-100%) (page 13, line 17). Note also analyses allowed for variation in the amount of seed consumed at different colonies. No changes made to text.



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