Reproductive success of house sparrows along an urban gradient

W. J. Peach[1], K. E. Vincent[2], J. A. Fowler[2] & P. V. Grice[3]

1 Royal Society for the Protection of Birds, UK Headquarters, The Lodge, Sandy, Bedfordshire, UK
2 Department of Biological Sciences, De Montfort University, Leicester, UK
3 Natural England, Northminster House, Peterborough, UK

Abstract

Recent large declines in house sparrow *Passer domesticus* L. populations in many European towns and cities have generated much speculation as to possible environmental causes, although empirical insights have been lacking. We measured reproductive success in a declining house sparrow population along an urbanization gradient in Leicester, England, and used mixed models to identify correlates of nesting success. A stochastic simulation approach was developed to estimate annual reproductive success when the number of breeding attempts was unknown, and to assess the sensitivity of reproductive success to variation in different environmental factors. During 2 out of 3 years, reproductive output was lower than the predicted threshold required for population stability. Years of inadequate reproduction were characterized by lower chick survival and body mass at fledging (a predictor of post-fledging survival). Factors associated with reduced reproductive output included low ambient temperatures, extremes of rainfall, high levels of vegetable material in the diet (all affecting chick survival and body mass), low aphid densities (an important component of chick diet) and high concentrations of air pollution from traffic (affecting chick body mass). Reproductive failure linked to inadequate invertebrate availability provides a plausible demographic mechanism accounting for declines in urban–suburban house sparrow populations. Increased traffic volume and vegetation removal are candidate causal factors in these declines although the mechanism underlying the former is unclear. Increasing densities of key invertebrate prey away from major roads should be an objective of conservation management aimed at urban–suburban house sparrows. This study illustrates the utility of mixed models for the analysis of individual sibling survival and of stochastic simulation for modelling reproductive success in multi-brooded animals.

Introduction

Evidence is mounting for large reductions in house sparrow *Passer domesticus* L. populations in many European towns and cities. In urban–suburban Britain, the decline appears to have started in the mid-1980s and continued throughout the 1990s (Summers-Smith, 2003; Robinson, Siriwardena & Crick, 2005). The best-documented change has occurred in London where numbers of breeding sparrows declined by 60% between 1994 and 2004 (Raven, Noble & Baillie, 2005). Smaller-scale surveys suggest losses of 85% in Kensington Gardens, London (1925–1995), 99% in suburban Glasgow (1959–1997), 90% in an Edinburgh park (1983–1998) and 75% in suburban Hamburg (1991–1999) (Summers-Smith, 1999; Dott & Brown, 2000; Mitschke, Rathje & Baumung, 2000). The house sparrow has recently been added to the list of priority species in the UK Biodiversity Action Plan and

its European status is no longer considered secure (Baillie *et al.*, 2007).

Such large and rapid losses of a familiar garden species have stimulated considerable speculation as to possible environmental causes of the decline (McCarthy, 2000; Summers-Smith, 2003; Beckerman, Boots & Gaston, 2007). Earlier declines of house sparrows on British farmland have been attributed to reduced availability of winter seed and grain linked to changes in agricultural practices (Hole *et al.*, 2002) but equivalent empirical studies in urban–suburban habitats are lacking. Small-scale studies of a declining suburban house sparrow population in Hamburg, Germany suggest brood starvation might have been caused by a lack of aphids (Aphidoidea) and ants (Formicidae) as chick food close to nests (Bower, 1999; Mitschke *et al.*, 2000). Extensive monitoring of house sparrow breeding success in Britain has highlighted a reduction in average maximum brood size

(from *c*. 3.5 in the late 1980s to 2.7 in 2003; Baillie *et al.*, 2007), suggesting that mortality of young chicks may be a widespread and increasing phenomenon. Summers-Smith (2003, 2007) speculates that the timing of population decline and the local re-distribution of nesting sparrows are consistent with an impact of vehicle exhaust emissions on house sparrows possibly via their invertebrate prey. Vehicle emissions are known to have a variety of impacts on plant physiology and growth but effects on invertebrates are less well understood (Bignal, Ashmore & Power, 2004). Emissions most likely to impact ecological systems include nitrogen oxides, volatile organic compounds, polycyclic aromatic hydrocarbons, metals and particulates (Bignal *et al.*, 2004).

The current study addressed three main questions. First, is annual productivity in suburban and rural garden-nesting house sparrows sufficient to maintain population size and does it therefore constitute a potential demographic cause of population decline. Second, does nutritional stress (as reflected through chick mortality and body condition) limit reproductive success, and third, what are the relative impacts on reproductive success of prevailing weather, habitat composition and air pollution from vehicle emissions within the vicinity of the nest. To answer these questions, we studied house sparrow reproductive success along an urban–suburban–rural gradient to ensure a wide range of variation in key ecological variables (McDonnell & Pickett, 1990; Theobald, 2004).

Materials and methods

Nest monitoring and covariates of nesting success

During 2001–2003 we studied reproductive success in a declining population of house sparrows breeding in artificial nest boxes in nine study areas in and around the city of Leicester, England. Nest boxes were erected in localities known to support house sparrows but occupancy rates varied between study areas (see Supporting Information Appendix S1). Boxes were fixed to the sides of buildings (usually two to four boxes per property, usually a domestic house), 4–5 m above ground level and within 10–20 m of roads. The distribution of occupied nest boxes was determined by the presence of sparrows, the willingness of residents to accept boxes and box occupancy rates. Nest histories were gathered for 258 nesting attempts from 104 nest boxes located across a range of urban (i.e. no private gardens within 100 m; four nesting attempts in 2001, two in 2002 and two in 2003), suburban (private gardens within 100 m; 9, 69 and 107) and rural (private gardens and farmland within 100 m; 6, 21 and 38) localities. Nest boxes were inspected at least once every 7 days between early April and mid-August to ensure that most breeding attempts were located during the egg stage and the fates of most nests were established with certainty. Censuses of adult males (two early morning surveys between February and May, covering 973 ha of urban, suburban and rural habitat) indicated a 9%

decline in breeding numbers between 2001 and 2002, and a further 21% decline between 2002 and 2003 (Vincent, 2006).

For each nest we calculated as many of the following parameters that could be determined with certainty: first egg date (assuming one egg is laid each day and an incubation period of 11 days; Summers-Smith, 1963), maximum clutch size, hatch date (observed or estimated from chick feather development), proportion of eggs hatched and the number of young fledged. Infertile eggs and dead chicks were usually found in the nest. Marking the legs of young chicks (2–6 days old) with indelible ink and older chicks (7–10 days) with individually numbered aluminium rings allowed the fates of individual chicks to be determined. Chicks were weighed (to the nearest 0.1 g) and measured (tarsus length to the nearest 0.1 mm). Many chicks produced faecal samples when handled and these were preserved in 70% alcohol for subsequent determination of the relative abundance of vegetable material in the chick diet, a simple measure of diet quality (Vincent, 2006). A binocular microscope was used to estimate the percentage cover of vegetable material (fragments of mainly bread, peanuts and seed) in each of 36 segments marked on a glass Petri dish across which the faecal remains were evenly spread.

Habitat composition was mapped within a 70 m radius of each occupied nest box, a distance that included 95% of foraging by provisioning adults in suburban Hamburg (Mitschke *et al.*, 2000). Seven habitat categories were recognized: deciduous shrubs, evergreen shrubs, ornamental shrubs and flowerbeds, trees, grass and weedy areas, vegetable patches and arable farmland, concrete/buildings. These categories were simplified using principal components analysis (PCA) in which the first axis (HAB1) accounted for 40% of variation in habitat composition across localities and reflected relatively large areas of grass (eigenvector = 0.45), deciduous shrubs (0.45) and trees (0.42) and relatively small areas of concrete (−0.53). A second axis (HAB2) accounted for a further 23% of the variation in habitat composition and reflected relatively large areas of evergreen shrubs (0.47) and concrete (0.31) and relatively small areas of arable (−0.65) and grass (−0.35). Habitat composition was only mapped in the year a nest box was first occupied, as there were no substantial habitat changes in subsequent years.

Air pollution data for Leicester were available from Atmospheric Dispersion Modelling Software (ADMS Urban version 1.6; Cambridge Environmental Research Consultants, 2001) that integrates point source air pollution data, traffic flows and meteorological data to predict spatial variation in air pollutant concentrations. Year-specific average daily concentrations of nitrogen dioxide (NO_2) covering the period March–September were available for each postcode area in our study (a UK postcode typically includes all the properties within a single suburban street; the median area of the 35 occupied postcodes in our study was 1.9 ha). Measures of several other air pollutants from vehicle emissions were highly correlated with NO_2 so were not considered further. NO_2 concentration declines rapidly with distance from roadside, falling by about 40% over the first

20 m and reaching background levels at about 100 m (Bignal *et al.*, 2004). Average NO_2 levels varied markedly between postcodes within our study areas (Supporting Information Appendix S1).

Aphids are important components of sparrow chick diet during June and July (Seel, 1969; Bower, 1999) and in 2003 we assessed the relative abundance of aphids during late June and July within the home ranges of 32 sparrow nests. These nests were selected to represent the full range of the urbanization gradient (mean NO_2 ranged between 16.9 and 29.2 μg NO_2 m^{-3} compared with 16.9–32.7 μg NO_2 m^{-3} for the full set of occupied nests in 2003). For each home range, we scored aphid abundance on 30–40 deciduous trees and shrubs, and 35–50 herbaceous plants and vegetables within 100 m of the nest. An ordinal rank abundance score (0 = no aphids, 1 = 1–15 aphids, 2 = 16–30 aphids, 3 = 30 + aphids) was assigned to individual herbaceous plants and to 10 randomly selected growing shoots to characterize individual trees and shrubs. Aphid scores were summed across plants within home ranges and expressed as the percentage of the maximum possible score.

Analytical methods

Generalized linear mixed models (GLMMs; Brown & Prescott, 1999) were used to identify correlates of reproductive success and chick condition. These analyses allowed for the non-independence of successive broods in the same box in the same year, or of individual chicks from the same brood, by declaring nest box or brood, respectively, as random factors. Declaring brood as a random factor allows the study of survival of individual chicks rather than the usual whole nest or brood (Mayfield, 1975; Johnson, 1979). This is particularly useful for species like house sparrow where partial brood mortality is common and where covariates relating to individual chicks (e.g. faecal samples) are available. The random brood term represents factors that influence the fates of all young within the same brood simultaneously and equally. Our approach is equivalent to a repeated measures model with equal variance and covariance between the fates of individual young within a brood [i.e. a compound symmetry covariance structure (Brown & Prescott, 1999)]. Study area was also declared as either a random (preferred) or fixed (if the random term failed to converge) factor to allow for the spatial clustering of nest sites. Mixed models carry an assumption that the random terms are normally distributed and histogram plots suggested this was reasonable for our data.

Dependent variables (normal errors unless stated otherwise) were clutch size, whole nest survival at the egg stage (binomial trials with logit link), the proportion of eggs hatching from each clutch excluding complete nest failures (binomial trials), daily survival rates of individual chicks (binomial trials), mean brood body condition 2–6 days after hatching and mean brood tarsus length and body mass 10–12 days after hatching. The body condition analysis involved modelling residuals from the strong, linear relationship between the logarithm of tarsus length and the

logarithm of body mass ($F_{1,144}$ = 805.2, $P < 0.0001$, R^2 = 0.85; Bradbury *et al.*, 2003; Schulte-Hostedde *et al.*, 2005). In order to reflect the full range of environmental conditions along our urbanization gradient, all 2002 and 2003 nest histories were included in the GLMM analyses, while the relatively small sample of nests from 2001 was excluded.

Initially the following set of 'nuisance' variables were screened for possible effects on dependent variables: year (2002 or 2003), period ('early' = first egg laid before the end of May, 'mid' = first egg laid during June, 'late' = first egg laid during July or August), average daily maximum temperature and rainfall (nest stage specific), brood size and chick age (the latter two for brood condition and body mass only). One-year-old house sparrows have lower nesting success than older birds (Summers-Smith, 1963; Hatch & Westneat, 2007). In case first time breeders were more likely than older birds to occupy newly available nest boxes, we tested whether dependent variables differed between first and subsequent years of nest box occupation but this was never significant. Having allowed for the effects of any significant nuisance variables, we then tested for relationships between dependent variables and habitat composition (two PCA axes), NO_2 levels and, for subsets of nests, the proportion of vegetable material in chick faeces and the abundance of aphids within 100 m of the nest. Variables were added to models using a step-up approach (most significant predictors first), checking for non-linear relationships (quadratic term in the presence of the linear term) and plausible interactions (i.e. between year and all other predictors, between period and habitat, NO_2, vegetable material and aphids, between temperature and rainfall and between habitat variables and NO_2, vegetable material and aphids). Inter-correlations between predictor variables were generally weak, the strongest being between HAB1 and NO_2 concentration ($r = -0.49$, $P < 0.001$). However, there were no instances where these two variables could substitute for each other as significant predictors of nesting success.

All GLMMs were fitted using procedures MIXED and GLIMMIX of SAS version 9.1 using the Satterthwaite approximation for estimating degrees of freedom (Littell *et al.*, 1996). As information theoretic approaches cannot generally be used to assess the importance of fixed factors in mixed models (Verbeke & Molenberghs, 2000; Gurka, 2006), Wald tests were used to select significant predictors of nesting success.

Stochastic simulation model of annual reproductive success

House sparrows typically make up to four nesting attempts each year (Summers-Smith, 1963), but we lacked direct measures of the numbers of attempts per pair. To estimate average annual reproductive output per breeding pair we developed a simulation model of nesting behaviour that extended the approach of Green *et al.* (1997) and Ratcliffe, Schmitt & Whiffen (2005). The model used observed distributions of start dates (the date of completion of the first clutch) and stop dates (the date after which no further

clutches were laid), and observed intervals between successive nesting attempts, all taken from individual nest box histories, to simulate re-nesting behaviour. In order to minimize any influence of sparrows switching nest sites between successive breeding attempts, we restricted start dates to those that occurred during the population-wide periods for known first and second nesting attempts in individual boxes. This assumes that any later 'first' attempts involved adults switching nest sites after their first attempt. Although a few genuinely late first attempts, perhaps by first-time breeders (Hatch & Westneat, 2007), may have been misclassified as second attempts, any consequent bias will have inflated estimates of reproductive success and therefore rendered our conclusions about their adequacy conservative. The observed seasonal distribution of nesting attempts (across eleven 10-day periods) was similar to that predicted by the simulation model (e.g. Kolmogorov–Smirnov tests for suburban nests: $D = 0.086$, $P = 0.72$ for 2002, $D = 0.098$, $P = 0.25$ for 2003) suggesting any bias was negligible.

The simulation model allocated a breeding female a start date, stop date and replacement period randomly selected from normal distributions defined by mean and standard deviation (SD) dates observed in Leicester. Stop date was constrained not to be later than 10 August (the latest observed nest initiation was 1 August). Clutch size was allocated according to the observed distribution and laying period was clutch size minus 1 day. The incubation period was fixed at 11 days and the chick period at 14 days (Summers-Smith, 1963). Observed daily whole clutch (Mayfield, 1975) failure rates were applied to each day of the laying and incubation period by testing whether a random probability exceeded the clutch survival rate until it failed or hatched. If the nest survived the incubation period, a random probability was generated for each egg and the egg was considered infertile or addled if this probability was below the observed rate of unviable eggs. In the same way, each chick was then subjected to an observed daily chick survival rate until all members of the brood were dead or at least one had reached fledging age (14 days old). The model then predicted survival during the 10 days following fledging (to independence) using the empirical relationship between body mass at 13 days old and subsequent survival (logit survival $= 0.2348 \times$ body mass $- 5.1005$) derived from Hole (2001). Body mass of chicks surviving to 13 days old was selected at random from a normal distribution based on observed mean and SD body mass statistics. When a nesting attempt ended, the replacement period was added to the estimated failure or fledging date and as long as this did not exceed the stop date, a subsequent nesting attempt was initiated. Observed replacement periods did not differ following successful and unsuccessful nests. When the stop date was exceeded, the total number of fledged and independent young reared by each pair was determined. The model simulated total annual productivity for a population of 100 sparrow pairs 4999 times, providing estimates of mean (plus 95% confidence intervals) population level productivity incorporating demographic stochasticity. Separate simula-

tions were run for nests in suburban and rural localities in 2002 and 2003 (the few urban nests were excluded), and for all 19 nests in 2001 (parameter estimates used in these simulations are listed in Supporting Information Appendix S2). Our estimates of reproductive success (measured and simulated) are compared with those from previous studies of house sparrows in Britain (Seel, 1970; Hole, 2001; Crick & Siriwardena, 2002).

By combining productivity estimates from the simulation model with published survival estimates for British house sparrows, it was possible to predict whether productivity was sufficient to maintain population size. The best available survival estimates for British house sparrows are derived from the entire national sample of ringing recoveries (habitat-specific estimates are not available) and cover the period 1976–1994 (Siriwardena, Baillie & Wilson, 1998). Many of the sparrows contributing to these survival estimates are likely to have been ringed in suburban and rural gardens where sparrow numbers were known to be declining for all (suburban) or most (rural) of this period (Robinson *et al.*, 2005). Owing to uncertainties over the average date of sparrow ringing, the exact starting dates of Siriwardena *et al.*'s (1998) 'annual' survival periods are unknown (survival periods ended on 15 July). House sparrows are identifiable as juveniles only until the completion of post-juvenile moult in September (Ginn & Melville, 1983), and we suggest that the average juvenile ringing date in Britain is likely to fall between 15 July and 15 August. We allowed for the period between the average date on which Leicester fledglings were expected to reach independence (30 June) and the start of the first-year survival period, by assuming average juvenile ringing dates of 15 July and 15 August and then applying Siriwardena *et al.*'s (1998) 'first-year' survival estimate (0.333) to the period between the average date of independence and the presumed average date of juvenile ringing (i.e. 15 or 46 days, respectively). Assuming annual adult survival of 0.50 (Siriwardena *et al.*, 1998), we estimated that the average number of independent young that each breeding house sparrow pair must raise each year in order to maintain stability of adult populations lies between 3.14 (average ringing date = 15 July) and 3.45 (15 August). Assuming survival between fledging and independence to average 0.62 (Hole, 2001), *c.* 5.1–5.6 young need to be fledged by each breeding sparrow pair each year. Our approach to assessing the adequacy of reproductive output assumes that all adult sparrows attempt to breed each year. Although non-breeding adults have been recorded in house sparrow populations (Summers-Smith, 1963), information on their relative abundance is lacking. The presence of non-breeding adults in our study populations would cause us to underestimate the threshold level of reproductive output required to maintain population stability, and would therefore render our conclusions about the adequacy of predicted reproductive output conservative.

The simulation model was also used to assess the sensitivity of annual productivity to variation in the environmental factors identified in GLMMs to be correlated with different components of reproductive success. Our aim was

to assess the pattern and relative magnitude of the potential impacts of the various environmental correlates on overall reproductive success rather than the component traits considered in GLMMs. Numerical relationships between the various components of reproductive success and environmental variables were incorporated into the model with any non-sensitive components being fixed to their observed means in 2002. Although single-variable perturbation approaches have their limitations (e.g. Katzner, Bragin & Milner-Gulland, 2006), they provide a useful means of assessing the form and relative importance of multiple additive predictors in GLMMs (e.g. Milsom *et al.*, 2000).

Results

Absolute levels of reproductive success

From an average clutch size of 4.04 eggs in all 3 years, 77% of eggs hatched and 65% of chicks fledged, resulting in an average of 2.02 chicks fledging per nesting attempt. Twenty-five per cent of all nesting attempts failed to fledge any

young, with a further 9 and 22% of nests fledging one and two young, respectively. Most eggs that failed to hatch appeared to be infertile and most chick mortality (72%) occurred within the first 4 days after hatching and appeared to be caused by starvation. No cases of nest predation were recorded.

The mean number of young fledged per nesting attempt varied significantly between years ($F_{1,228} = 10.3$, $P < 0.005$) with fewer young being fledged in 2003 than in 2001 or 2002 (Table 1). The number of nesting attempts predicted by the simulation model was similar to that recorded in previous studies (Table 1; Summers-Smith, 1963). Predicted post-fledging survival was higher than or similar to that for a declining farmland population in Oxfordshire (Hole, 2001; Table 1).

In 2001 and 2003, the average annual production of fledglings and independent young per pair was lower than that recorded in farmland populations during the 1960s and 1990s, and much lower than the predicted threshold required to maintain population stability (Table 1, Fig. 1). In 2002, reproductive success was at (suburban) or above

Table 1 Components of reproductive success compared across studies

Location	Oxfordshire[a]	Oxfordshire[b]	Oxfordshire[b]	Britain[c]		Leicester[d] (this study)				
Time period	1961–1964	1967–1971	1998–2000	1970–2000		2001	2002	2002	2003	2003
Habitat	Sub	Farm	Farm	Sub	Rur	Mix	Sub	Rur	Sub	Rur
Population trend	Stable?	Stable	Declining	Stable/decline		Declining				
Component										
Fledglings per attempt	1.6	2.3	2.6	2.6	3.1	2.1	2.2	2.6	1.4	1.7
Nesting attempts per pair[e]	2.1/2.5[f]	2.4	2.1	–	–	2.3	2.4	2.3	2.4	2.0
Fledglings per pair	3.4/4.0[f]	5.4	5.7	–	–	4.7	5.4	6.1	3.4	3.3
Chick mass on day 13	23.8	23.8	23.3	–	–	23.5	24.8	27.2	23.4	24.7
Post-fledging survival[g]	0.62	0.62	0.59	–	–	0.60	0.67	0.78	0.60	0.66
Independent young per pair	2.1/2.5[f]	3.4	3.4	–	–	2.7	3.6	4.5	2.0	2.1
Probability <3.14 independent young raised per pair[h]	–	–	–	–	–	1.0	<0.01	0.00	1.0	1.0
Population multiplication rate[i]	1.11/1.21[f]	1.44	1.04	–	–	0.93	1.07	1.22	0.82	0.83

Habitats are farmland (Farm), suburban (Sub), rural (Rur) and mixed suburban and rural (Mix); population trend summarises changes in population size at the time of the study.

[a]From Seel (1970). Based on 911 nest histories. Population status unknown but probably stable.

[b]From Hole (2001). Based on *c.* 372 (1967–1971) and 272 (1998–2000) nest histories.

[c]From Crick & Siriwardena (2002). Based on 817–1102 (Sub) and 325–541 (Rur) nest histories.

[d]All components of nesting success (except chick mass and post-fledging survival) are derived from the simulation model. See 'Materials and methods' for sample sizes.

[e]The observed mean numbers of nesting attempts per nest box were: 1.2 in 2001, 1.9 (Sub) and 2.1 (Rur) in 2002, and 2.1 (Sub) and 1.7 (Rur) in 2003.

[f]Seel's (1968) estimate of 2.13 attempts per nest box made no allowance for sparrows switching nest sites between attempts. Productivity estimates are therefore presented for this minimum estimate and for a corrected estimate based on the observed difference between this and the simulated number of attempts per pair derived from the Leicester data from 2002–03 (i.e. 2.13 + 0.34 = 2.47 attempts). The equivalent correction from the Oxfordshire farmland study was +0.68 in 1999 and +0.55 in 2000 (D. Hole, pers. comm.).

[g]Predicted from chick mass on day 13 (Hole, 2001).

[h]From the distribution generated from 4999 simulations for a population of 100 pairs (see 'Materials and methods'); 3.14 independent young is the productivity needed to maintain population size assuming an average ringing date for juvenile house sparrows in Britain of 15 July (see 'Materials and methods').

[i]Predicted from the number of surviving independent young, assuming adult and first-year survival rates of 0.582 and 0.502 respectively during 1961–75, and 0.5 and 0.318 after 1975 (from Siriwardena *et al.*, 1998). First-year survival estimates have been adjusted to include the period between the mean date of juvenile independence (estimated from the Leicester data to be 30 June) and the average ringing date of juvenile sparrows in Britain (assumed here to be 15 July; see 'Materials and methods').
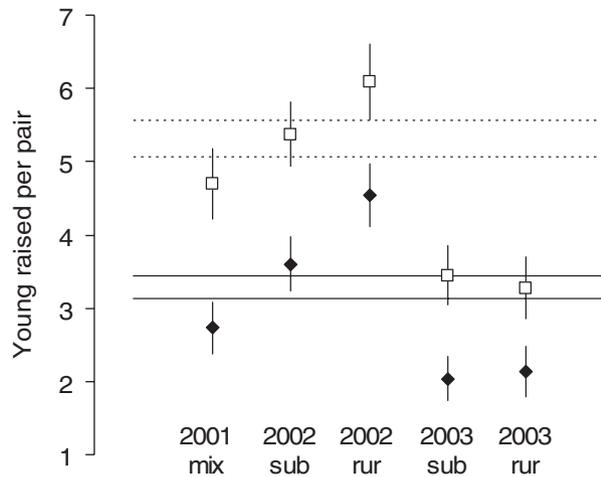
Figure 1 Variation between years and suburban (sub) and rural (rur) localities in the number of young reared to fledging (open squares) and to independence (filled diamonds) per house sparrow *Passer domesticus* L. pair per year (errors bars show 95% confidence intervals). The 2001 sample was a mix of nests from rural, suburban and urban localities (see 'Materials and methods'). Horizontal lines show the productivity required to balance annual mortality estimated from British ringing recoveries. Dashed lines show the required number of fledged young and continuous lines the required number of independent young. The two lines of each type reflect different assumed average ringing dates for British juvenile sparrows (lower line = 15 July, upper line = 15 August; see 'Materials and methods').

(rural) the predicted threshold for population stability (Fig. 1). The main components of reproductive success that differed between years of adequate (2002) and inadequate (2001 and 2003) reproduction were chick survival (lower in 2003; daily rate of 0.953 compared with 0.982 in 2001 and 0.977 in 2002) and post-fledging survival (lower in 2001 and 2003, Table 1). The proportion of eggs that hatched was only slightly higher in 2002 (0.80 compared with 0.76 in 2001 and 2003). The higher reproductive success in rural (compared with suburban) localities in 2002 was a consequence of higher rates of egg fertility, chick survival and post-fledging survival (Supporting Information Appendix S2).

Correlates of reproductive success

Clutch size and chick survival varied seasonally while egg stage survival, chick survival and body mass before fledging varied between years (Table 2). Low temperatures and wet (and very dry) weather were associated with reduced chick survival, brood condition at 2–6 days and brood body mass at 10–12 days of age. The proportion of eggs hatching and chick survival (after allowing for variation in aphid abundance) were weakly related to habitat composition around the nest (HAB1 in Table 2).

Brood body condition at 2–6 days old, and brood tarsus length and body mass at 10–12 days old were all strongly and negatively related to local NO_2 concentration (Table 2). An analysis of brood condition at 10–12 days old (using the same method used for younger chicks) highlighted a marginally significant negative relationship with NO_2 ($P = 0.07$). Chick body mass at day 13 is a strong predictor

Table 2 Predictors of components of nesting success and chick body condition in suburban–rural house sparrows *Passer domesticus* L.

Breeding parameter	Number of nests or chicks	Predictors: Temporal/weather	Environmental
Clutch size	242	PER***	
Whole nest survival at egg stage	228	YR*	
Proportion of eggs hatching	202		**HAB1**[(*)]
Chick survival	735	YR***, PER***, YR x PER* **TM***, TM^2*, **RF***, RF^2 ***	
	206[a]	**RF***, RF^2 ***	VEG***
	110[b]	**RF***, RF^2 ***	**APHID****, **HAB1***
Brood condition at 2–6 days old	146	**TM***, TM^2***, **RF***, RF^2***	NO_2***
Brood tarsus length at 10–12 days old[c]	75	YR***, RF, RF^2*	NO_2***
Brood body mass at 10–12 days old[c]	75	YR***, RF, RF^2*	NO_2***
	29[a]		NO_2*, VEG**

Predictors are year (2002, 2003: 'YR'), period (early, middle or late breeding season: 'PER'), temperature (TM) and rainfall (RF), local habitat composition (first principal component: HAB1), proportional of vegetable material in chick faeces (VEG), local abundance of aphids during June–July 2003 (APHID) and local summer atmospheric concentration of nitrogen dioxide (NO_2). Bold type indicates significant positive relationships, ordinary type indicates negative. Squared terms indicate quadratic relationships.

[(*)] $P < 0.07$.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.005$.
[a] Analyses restricted to chicks/broods from which faecal samples were available.
[b] Analyses restricted to chicks reared from localities that were surveyed for aphids during June–July 2003.
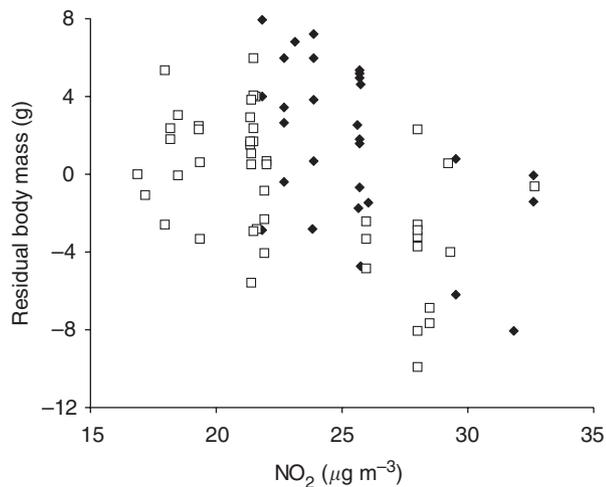[c] Models include significant brood age factors.

Figure 2 Relationship between mean brood body mass at fledging (allowing for chick age and rainfall effects) and local summer concentrations of nitrogen dioxide in 2002 (filled diamonds; $r = -0.52$, $P < 0.005$) and 2003 (open squares; $r = -0.53$, $P < 0.001$).

of post-fledging survival probability (Hole, 2001). The relationship between brood body mass at 10–12 days old and local NO_2 concentration (Fig. 2) predicts the former to average 24.6 g at 20 $\mu g\, NO_2\, m^{-3}$ and 19.3 g at 30 $\mu g\, NO_2\, m^{-3}$ (Fig. 2), which equates to predicted survival over the 10-day post-fledging period of 0.66 and 0.36, respectively.

Chick survival and body mass at 10–12 days old were both strongly related to the quality of chick diet (Table 2). Chicks for which vegetable material comprised <10% of faecal volume had an expected survival probability over the entire 14-day hatching to fledging period of 0.79 compared with 0.27 for chicks whose faecal samples comprised 50% or more vegetable material (Fig. 3a). During June and July 2003, daily chick survival was higher in localities with abundant aphids (Fig. 3b), and this equates to expected survival over the 14-day chick period of 0.82 and 0.36 in the highest and lowest aphid abundance categories, respectively.

Single-variable perturbation analyses suggested relatively strong relationships between reproductive output and temperature, rainfall and NO_2, and a weaker relationship with habitat composition (Fig. 4). Variation across the observed 90 percentile range of chick stage ambient temperatures could account for 2.2 additional independent young per pair per year, compared with 2.1 for the equivalent range of NO_2 levels, 1.8 for rainfall and 0.5 for habitat composition (Fig. 4). Given that our best estimate of the threshold level of productivity necessary for population stability is 3.1–3.5 independent young per pair per year (see 'Materials and methods'), variation in temperature, rainfall and NO_2 all have the potential to have biologically significant impacts on reproductive success in suburban house sparrows.

Discussion

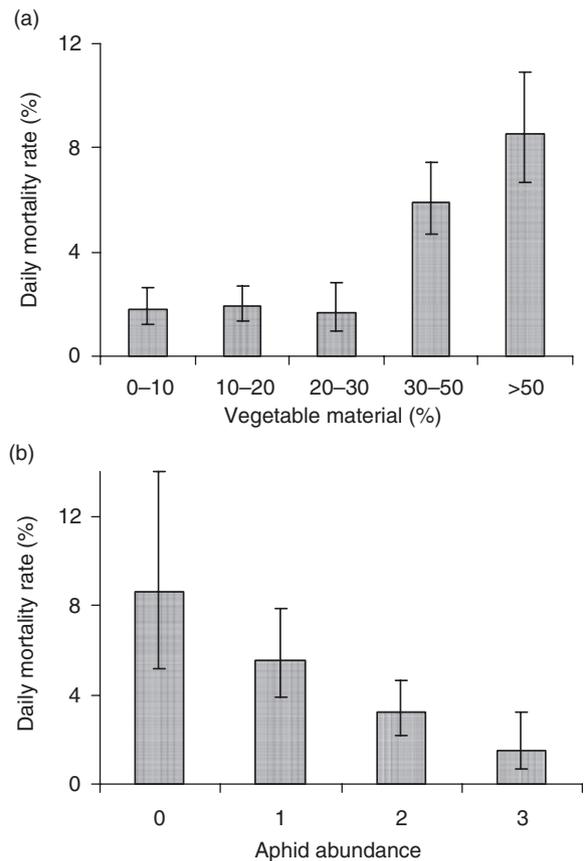This study highlights inadequate reproductive success as a potential cause of population declines among suburban

Figure 3 Relationship between daily chick mortality ($\pm$ SE) and (a) the extent of vegetable material in faecal samples and (b) the relative abundance of aphids within 100 m of nests during June and July 2003. Aphid scores are grouped into four bins reflecting low (0) to high (3) relative abundance.

house sparrows. One previous study of suburban house sparrows found similarly low reproductive success to that in Leicester (Seel, 1970), although daily inspection of nests in that study might have affected nest outcomes. Higher over winter survival during the 1960s (Siriwardena *et al.*, 1998) may have rendered this apparently low reproductive success sufficient to maintain population size (Table 1).

The main demographic components accounting for low reproductive success were higher chick mortality during the first week after hatching (2003) and reduced post-fledging survival (2001 and 2003, inferred from body mass prior to fledging), both of which imply nutritional stress affecting chicks as the most likely proximal limiting factor. House sparrow chicks are fed mainly invertebrates especially during the first week after hatching (Summers-Smith, 1963) when so much of the mortality in this study occurred. In Leicester, adult Tipulids (Diptera), weevils (Curculionidae), spiders (Araneae), aphids and ants were the main invertebrate prey (Vincent, 2006), while grasshoppers (Orthoptera) and moth (Lepidoptera) larvae have been more prominent in other studies (Seel, 1969). Direct evidence for an influence of invertebrate availability on reproductive success is
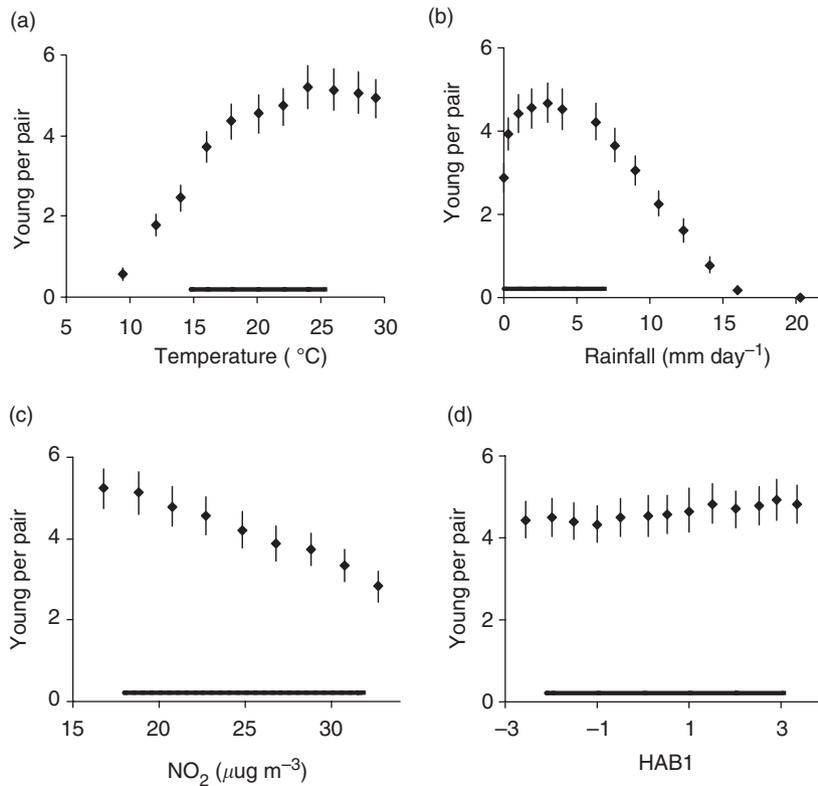
Figure 4 Predicted impacts of summer (a) temperature, (b) rainfall, (c) local NO_2 and (d) habitat composition (first principal components analysis axis) on the number of independent young raised per house sparrow *Passer domesticus* L. pair per year. The number of young raised (vertical lines are 95% confidence intervals) was derived from a model simulating re-nesting behaviour (see text). Thick horizontal lines show the ninety percentile ranges of the environmental variables.

provided by the strong negative relationship between the proportion of vegetable material in chick faecal samples, and the positive relationship between local aphid abundance and chick survival (Fig. 3). The latter may reflect a positive association between the abundance of aphids and a range of potential invertebrate prey including ants, various Diptera, Coleoptera and Neuroptera (Dolling, 1991), rather than any dependence of sparrow chicks on aphids.

The quality of the chick diet probably explains the marked differences in chick survival and brood body mass between 2002 and 2003 (which were evident after allowing for any possible effects of weather and NO_2, Table 2). The proportion of vegetable material in chick faeces was significantly higher in 2003 than in 2002 (Vincent, 2006) and when this measure of chick diet quality was included in GLMMs, the previously significant 'year' effect disappeared. It is not clear why invertebrate prey might have been less available in 2003 than in 2002 (conditions in 2003 were warmer and drier than in 2002 but not exceptional). Invertebrate availability has previously been proposed as a factor limiting reproductive success of house sparrows, great tits *Parus major* L., blue tits *Parus caeruleus* L. and starlings *Sturnus vulgaris* L. in urban–suburban habitats (Seel, 1970; Cowie & Hinsley, 1987; Mennechez & Clergeau, 2006). Nutritional stress is also the most plausible explanation for the recent reduction in average maximum brood size from an extensive sample of house sparrow nests from across Britain (Baillie *et al.*, 2007).

The observed relationships between temperature and rainfall and chick survival and condition probably reflects a combination of direct physiological impacts (e.g. chilling) and indirect impacts on invertebrate availability. Low temperatures generally limit invertebrate activity and reproduction, while heavy rainfall may inhibit invertebrate activity and the foraging efficiency of birds (Cowie & Hinsley, 1987). Average maximum daily temperatures increased significantly (linear regression of mean monthly temperatures for May, June and July on year: $P = 0.006$) in Leicester from an average of 17.7 °C in 1961 to 19.1 °C in 2002 but there was no evidence of any similar trend in summer rainfall. By incorporating local historical daily temperature and rainfall records into our simulation model of sparrow nesting behaviour, we estimated the potential impact on reproductive success of observed long-term variation in breeding season weather conditions (Fig. 5). This suggests that the warmer summers of the 1980s and 1990s are likely to have been more conducive to successful reproduction in house sparrows, and are unlikely to have caused any reduction in breeding success. The slight reduction in the suitability of weather conditions since the late 1990s is a consequence of heavier rainfall during several of those summers (e.g. 1997).

Chicks in localities with high NO_2 levels tended to be smaller and lighter than those in localities with lower NO_2 levels (Table 2, Fig. 2). The observed differences in body mass were large enough to have had a relatively large impact
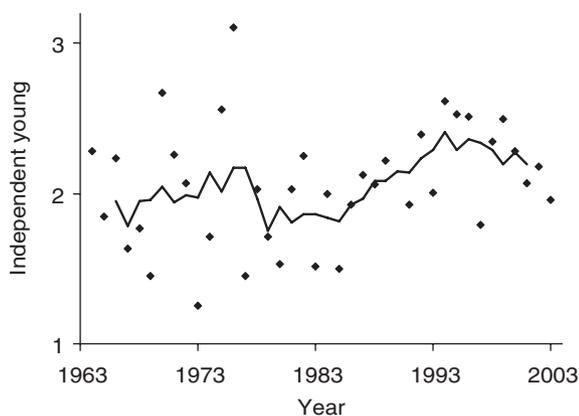
Figure 5 Predicted impacts of long-term variation in daily temperature and rainfall on annual reproductive success (number of independent young raised per pair) in Leicester house sparrows. Reproductive success is estimated from the re-nesting simulation model using average reproductive parameters and NO_2/HAB1 values for the years 2001–2003. The line shows the 5-year moving average.

on post-fledging survival (Hole, 2001) and thereby overall reproductive output (Fig. 4c). Our data provide a potential mechanism (i.e. nutritional stress) to account for a tendency for adult sparrows to be smaller and lighter in urban areas compared with counterparts in rural and suburban sites (Liker *et al.*, 2008). Road traffic is the main source of NO_2 in urban–suburban areas and levels of this pollutant can be considered an indirect measure of local traffic volume (Bignal *et al.*, 2004). We can think of three potential mechanisms through which air pollution from traffic or proximity to major roads might affect body mass in house sparrow chicks. First, some component of air pollution from traffic could be affecting invertebrate densities either directly or via effects on plant hosts (Bignal *et al.*, 2004). Several studies document increased densities of aphids close to roads (Spencer & Port, 1988; Bolsinger & Fluckiger, 1989), while effects of roads on other invertebrate groups are mixed (Przybylski, 1979; Muskett & Jones, 1980). Second, some component of air pollution from traffic (such as heavy metals or particulates) could have a direct toxic impact on chicks, either through ingestion of contaminated prey (e.g. Eeva, Lehikoinen & Nikinmaa, 2003) or through inhalation. Third, house sparrows are relatively vulnerable to mortality caused by collisions with moving vehicles especially during the breeding season (Heij & Moeliker, 1990; Erritzoe, Mazgajski & Rejt, 2003) and it is likely that sparrows nesting close to major roads suffer higher rates of such mortality. The death of one parent is likely to reduce food intake rates of chicks and thereby affect brood body mass. Higher aphid densities close to roads could potentially attract foraging parent sparrows to dangerous roadside locations.

UK traffic volume has increased by 82% since 1980 (20% since 1990), most of this caused by increases in car usage (Department for Transport, 2007). The levels of air pollution associated with traffic emissions probably peaked in Britain during the early 1990s and have since declined or stabilized (Bower *et al.*, 2006). Concerns are now focused on NO_x, particulate matter, ozone, ammonia and some lead replacement anti-knock agents such as methyl tertiary butyl ether (Cape *et al.*, 2004; Summers-Smith, 2007).

Management to promote invertebrate abundance in urban–suburban habitats is an obvious recommendation to draw from this study, although other unknown limiting factors might still constrain population recovery. House sparrow parents collect most invertebrate prey from deciduous woody vegetation, trees and grassland and make relatively little usage of evergreen or ornamental shrubs (Vincent, 2006). There is evidence of widespread recent losses of greenery from British cities as a consequence of development on green space, tree removal and the conversion of front gardens for parking (e.g. London Assembly, 2001, 2005, 2007). Management should therefore include the planting of native deciduous shrubs and trees especially those providing canopy cover above 2 m (Smith *et al.*, 2006). Allowing a diversity of grasses and forbs to set seed and remain *in situ* throughout the winter should promote the abundance of a range of foliar invertebrates including Dipterous flies, Lepidopteran larvae, spiders and Homopteran bugs (McNeill, 1973; Purvis & Curry, 1981; Morris, 2000). Given the uncertainty concerning the possible impacts of air pollution and/or vehicles on house sparrows, management to promote invertebrate abundance should initially be concentrated away from busy roads. Such advice needs to be targeted at the owners of private gardens and could be incorporated into local authority green space management plans.

Most previous studies of avian reproductive success have considered the survival of whole broods because the fates of individual young cannot be assumed independent (Mayfield, 1975; Johnson, 1979; Dinsmore, White & Knopf, 2002). Declaring brood as a random factor within a mixed model allows for the non-independence of sibling fates and the testing of individual covariates. Our approach could readily be extended to incorporate more complex forms of correlation within subject groups. For example, for species exhibiting hatching asynchrony where the condition and survival of offspring depends on hatch order, an autoregressive correlation structure (Brown & Prescott, 1999) might be more appropriate. The simulation approach has wide potential application to studies of multi-brooded animals because it overcomes the common problem of a lack of knowledge of the number of breeding attempts made per female, and because it allows direct comparison of the sensitivity of annual reproductive success to a range of candidate environmental factors. The main limitation to simulations of this sort will be a lack of detailed knowledge of key parameters such as the distributions of stop dates and intervals between nesting attempts. Even where such information is lacking, it would be possible to assess the sensitivity of productivity to a range of plausible parameter values (sometimes available from previous studies) and to explore relationships between productivity and environmental variables.

Acknowledgements

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Supporting Information

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

Appendix S1. Attributes of house sparrow (HS) study areas and nest box occupancy.

Appendix S2. Observed mean components of reproductive success used in stochastic simulation models.

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