Wild Bird Feeding in an Urban Area: Intensity, Economics and Numbers of Individuals Supported

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Abstract. Feeding wild bird is popular in domestic gardens across the world, with around half of households in the UK, North America and Australia doing so. Nevertheless, there is surprisingly little empirical information on many aspects of the activity. We sought to characterise garden bird feeding in a large UK urban area in two ways. First, we conducted face-to-face questionnaires with a representative cross-section of residents. Just over half fed birds, the majority doing so year-round and at least weekly. Second, a 2-year, longitudinal study recorded all foodstuffs put out by households on every provisioning occasion. In this way, we obtained the first year-round quantitative records of the amounts and types of wild bird food provided in individual gardens. A median of 127 g, equivalent to 628 kcal, was given daily per household (typically consisting of several food types). We estimated the daily cost of this provisioning level to be UK£0.35 per household based on the relative proportions of each food type. Provisioning level was not significantly influenced by weather or season. Comparisons between the data sets revealed significantly less frequent feeding amongst the feeders in the longitudinal study (assumed to be 'keen' feeders owing to their participation in this long-term study and numbers of food types provided) than the face-to-face questionnaire respondents, suggesting that questionnaires relying upon participants' estimates rather than records of provisioning may overestimate actual provisioning frequency. Assuming 100% uptake, the median provisioning level equates to sufficient supplementary resources across the UK to fully support 196 million individuals of a hypothetical average garden-feeding bird species (based on 10 common UK garden-feeding birds' energy requirements). This compares with an estimated total of 71 million breeding individuals of these 10 species in the UK (non-breeding numbers unknown). Taking the lowest provisioning level recorded (101 kcal/day) as a conservative measure, 31 million of these average individuals could theoretically be supported.

Key words: wild bird feeding, anthropogenic provisioning, urban ecology, human–wildlife interaction, citizen science, socioeconomic status, geodemographic classification

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INTRODUCTION

Diverse influences of deliberate anthropogenic provisioning of wild birds have been recorded, from improved over-winter survival rates (e.g. Jansson et al. 1981, Brittingham & Temple 1988a) and both increases and decreases in productivity (Robb et al. 2008, Harrison et al. 2010, Plummer et al. 2013b) to later singing at dawn (Saggese et al. 2011) and increased rates of disease transmission (e.g. Brittingham & Temple 1988b, Friend et al. 2001). Interspecific differences in the use of supplementary food may also alter the structure of bird assemblages e.g. leading to the return of Red Kites *Milvus milvus* as urban scavengers (Orros & Fellowes 2014, 2015; see Cannon et al. 2005 for other examples). Indirect effects in the form of local depletion of arthropod prey around garden bird feeding stations have also been demonstrated (Orros & Fellowes 2012, Orros et al. 2015).

Garden (backyard) bird feeding is a popular activity in many countries. Recent estimates indicate that close to half of households participate in the UK (48%; Davies et al. 2009), the USA (47%; US Fish and Wildlife Service 2006, US Census Bureau 2011) and Australia (36–48% in Queensland; Ishigame & Baxter 2007). In 2012, an estimated 166 000 tonnes of pet and wild bird food were sold in the UK (Pet Food Manufacturers' Association 2013). However, to our knowledge no quantitative data on the food provided for garden birds by individual households have been published (see also Fuller et al. 2012).

This type of information would allow the amount of energy being added to garden ecosystems and thus the numbers of individuals potentially supported to be estimated. This has relevance not only with respect to the birds directly targeted by garden-holders but also to other taxa. Many mammals also consume wild bird foods (e.g. rodents, particularly the Grey Squirrel *Sciurus carolinensis* and Brown Rat *Rattus norvegicus* in the UK; National Pest Technicians Association 2010, Bonnington et al. 2014).

The provision of anthropogenic food resources for wild animals is particularly relevant in urban areas. Alternative natural food sources are typically less available (Fuller & Irvine 2010) and domestic gardens can constitute a significant proportion of land cover, e.g. ~25% of various UK cities (Loram et al. 2007); 36% of Dunedin, New Zealand (Mathieu et al. 2007). Furthermore, the percentage of the world's human population inhabiting urban areas is continuing to rise past the recently reached 50% point (United Nations 2011a). This implies that anthropogenic energy inputs (such as wild bird food) will become increasingly biased towards such regions. The UK's towns and cities are thus useful locations in which to study garden bird feeding because of the country's combination of high levels of participation in the activity and a percentage of urban inhabitants well above the global average (80%; United Nations 2011b).

In the UK, the targets of garden bird feeding are typically small- to medium-sized granivorous and insectivorous passerines (e.g. European Robin *Erithacus rubecula*, Blue Tit *Cyanistes caeruleus*, Blackbird *Turdus merula* see Toms 2003, BTO 2013). Other taxa such as corvids (e.g. Magpie *Pica pica*) also commonly take food from gardens (Toms 2003) and meat-based diets are now deliberately provided in some areas (e.g. for Red Kites, Orros & Fellowes 2014, 2015). Surprisingly, the most recent UK data for seasonal variation in when food is provided are those published by Cowie & Hinsley (1988) indicating feeding during winter to be almost twice as common as in summer. However, the major national ornithological organizations, the British Trust for Ornithology (BTO) and the Royal Society for the Protection of Birds (RSPB), now advocate year-round feeding (Buczacki 2007). It therefore seems likely that Cowie & Hinsley's (1988) figures are no longer representative, particularly given that recent data from other countries with similar levels of household participation indicate that feeding is

predominantly year-round (Australia: Rolllinson et al. 2003; North America: Horn & Johansen 2013). Similarly, despite the substantial increase in the range of commercially produced foods in the UK over the last 25–30 years (Buczacki 2007), Cowie & Hinsley's (1988) data remain the most recent for the relative percentages of households providing different types of food. We are also unaware of any published estimates of the per-household cost of feeding wild birds.

We examined garden bird feeding in a large UK urban area at two scales: a large, face-to-face questionnaire of a cross-section of residents and a smaller, more focussed study recording actual feeding activity over 2 years (hereafter referred to as the 'longitudinal' study). Our aims were to: (1) gather baseline data on the extent and nature of garden bird feeding by residents, including seasonality of feeding; (2) obtain quantitative data on the types of food and amounts provided over time and use these to estimate the energy being added and the costs of provision, and examine seasonal patterns of resource provision; (3) compare feeding habits between the data sets and examine any differences; and (4) estimate the numbers of birds potentially supported by the resources provided.

METHODS

Study area
The study focussed on a 72-km^2 urbanized area in Berkshire, southern England, composed of the town of Reading (51°27'N, 0°58'W) and the contiguous parishes of Woodley, Earley, Tilehurst, Holybrook and Purley on Thames and the electoral ward of Shinfield North. It includes ~96 000 households (Office for National Statistics 2013) and is hereafter described as Greater Reading. In order to maximise sample size in the longitudinal bird-feeding study (described below), we included three households just outside the Greater Reading boundary (≤ ~1 km) but within adjacent areas.

Face-to-face questionnaire
We conducted questionnaires outside supermarkets across Greater Reading in order to investigate residents' wild bird-feeding habits. Questions included the seasonality and frequency of feeding and the number of foods provided. Frequency of feeding refers here and throughout this paper to how often participants put out bird food; we acknowledge that this does not give information

on whether or not any food remained from the previous feeding occasion. Questions on the Red Kite, a raptor recently reintroduced close by, were also included for another study (Orros & Fellowes, 2015) but are not discussed here.

Surveying took place from November 2010–January 2011. We selected 10 local supermarkets and varied the times and days of survey sessions for broad socioeconomic and lifestyle coverage. Completing the questionnaire took ≤ 5 min to encourage participation. Surveyors recruited participants without revealing the subject to avoid bias (Salant & Dillman 1994). Only one respondent per household was interviewed and all questionnaires were conducted by one of two surveyors.

We checked the socioeconomic representativeness of our sample because such factors have been shown to influence participation in bird feeding (Avilova & Eremkin 2001, Fuller et al. 2008, 2012). We compared our sample of respondents with SE England using CACI's A Classification Of Residential Neighbourhoods (ACORN) UK geodemographic classification system, which assigns households to categories by postcode based on census data (see Appendix 1 for brief category descriptions and CACI (2010) for further details). We selected ACORN over other possible classification systems for brevity because postcodes were already required to confirm residency within our definition of Greater Reading (data from responses with postcodes outside Greater Reading were excluded).

Longitudinal bird-feeding study
A 2-year study (1 June 2010−31 May 2012) was conducted in which volunteers recorded the amounts and types of all food provided for wild birds in their gardens. Households that had fed birds for at least 6 months were recruited by requests to participants of previous studies (Orros & Fellowes 2012, Thomas et al. 2012, 2014), a project website, local media and special interest groups. The participating households were situated across Greater Reading (and just outside; see Study area section) at varying distances from the town centre but were not evenly distributed because of the voluntary nature of the study. No household was more than ~3 km away from another participant. The distance between the two furthest apart households was ~10 km.

To maximise convenience for participants, either the mass or volume of the bird food provided could be recorded in either imperial or metric units, with measurements later converted by us into metric masses if appropriate. All food

subsequently removed (e.g. because of spoilage or during cleaning) was also recorded and accounted for in our calculations.

The study was split into eight 3-month seasons to allow on-going data analysis and updates for volunteers. Households were able to join or withdraw (including temporarily) to encourage participation. Nine participants in the first season missed the start date. Given the low sample size (see Results), we asked these households to start at the mid-point of this season and then doubled their data (masses of each food category prior to further calculations) for this season only.

In order to facilitate comparisons amongst gardens in our analyses, some similar foodstuffs were merged into categories (e.g. mixed seed, fat blocks/balls, fresh fruit). Kilocalorie (kcal) values for each food category were obtained from a selection of major suppliers (see Appendix 2). We then calculated the approximate kilocalorific values of all food categories from their masses. We used these data rather than masses to estimate the per-household provisioning means and the numbers of individuals supported and to investigate seasonal patterns of provisioning in order to avoid overestimation of energy provision by households providing low-energy-per-unit-mass foods such as fresh fruit.

We also obtained the prices of the food categories from major retailers (as of November 2014; Appendix 2), using means for the merged categories. The median daily cost of feeding was estimated by calculating the overall proportion of each food category by mass provided throughout the study and then multiplying these proportions by the median daily mass (g) provided per garden to give the relative mass for each food category per day. These were then multiplied by the cost per gram of each food category and summed to give the median cost per feeding garden per day. We note that this does not account for the costs of feeding equipment.

The possible influences of mean daily temperature and rainfall, season (the 3-month study seasons) and study year on the number of kilocalories provided were investigated. Local seasonal temperature and rainfall data were obtained from the University of Reading Atmospheric Observatory (51.442°N, 0.938°W; 66 m asl; see Table 1 in Results section).

Comparisons between data sets
We compared the number of foodstuffs and feeding frequency of households between the

face-to-face questionnaire and longitudinal study participants. We first compared the relative frequencies of daily, several times a week, weekly, less than weekly feeding (i.e. number of occasions on which food was put out; feeding frequencies of longitudinal study participants determined from provisioning records). Given the similarity of the first three categories and to facilitate comparison with previous studies (e.g. Cowie & Hinsley 1988, Ishigame & Baxter 2007, Davies et al. 2012, Lepczyk et al. 2012), we also compared levels of at least weekly versus less than weekly feeding.

Estimated numbers of individuals supported

The median and lowest numbers of kilocalories provided daily by our longitudinal study participants were used to estimate the numbers of individuals of various species potentially supported, assuming 100% uptake of the food provided by that species alone for each calculation. We acknowledge that this does not account for the dietary specializations or dominance hierarchies of the species selected (i.e. not all species/individuals will eat all of the food types provided or have equal access to resources: Sasvári 1988, Suhonen et al. 1992). In addition, although we accounted for spoiled food removed by participants, some food may not have been consumed (e.g. food falling out of feeders/discarded by birds during feeding bouts although note that some of this may be eaten by ground-feeding birds). We used the median as the data were not normally distributed and the lowest level as a conservative measure of support as participants were self-selected and therefore likely to be keener than the general bird-feeding population.

As examples of the species utilising supplementary food in the UK we selected the 10 bird species (see Table 2 in Results section for list) seen taking supplementary food by the greatest percentage of British Trust for Ornithology (BTO) Garden Bird Feeding Survey (GBFS) participants in winter 2012/13 (BTO 2013). We acknowledge that this does not directly relate to numbers of individuals. As several species typically feed within a single garden and their food preferences vary (Chamberlain et al. 2005, Ishigame & Baxter 2007), we also estimated numbers of a hypothetical 'average' UK garden-feeding bird. Its energy requirements were calculated by weighting the kilocalorie requirements of the 10 species by the percentage of GBFS gardens within which they were seen. This provided an estimate of the numbers supported given a mix of these species. For

comparison, we also estimated support for a bird-food eating mammal, the Grey Squirrel.

Statistical analyses

All modelling was carried out in R v.2.12.0 (R Development Core Team 2010).

The possible influences of mean daily temperature and rainfall, season and year on the kilocalories provided in the longitudinal feeding study were investigated using linear mixed-effects modelling (using package nlme: Pinheiro et al. 2010) with household as a random effect and study season nested within study year. Calorific data were log_{10}-transformed to meet assumptions of normality.

We performed Fisher's exact tests in R to compare the four feeding frequencies and two-tailed tests of two proportions in Microsoft Excel (2010) to compare at least weekly and less than weekly feeding between the face-to-face questionnaire and longitudinal study participants.

RESULTS

Face-to-face questionnaires

We obtained 503 useable responses from the Greater Reading area. Of these, 278 (55.3%) fed wild birds, equivalent to 53 088 households across Greater Reading.

Almost two-thirds of feeders fed year-round (n = 181), with most of the remainder provisioning only in autumn/winter (n = 91) and six only in spring/summer. The relative proportions of feeding frequencies (feeding daily, several times a week, weekly and less often) were similar for all feeding households combined (data not shown) but varied with the time of year at which households fed birds (Fig. 1). We only compared households feeding year-round and in autumn/ winter statistically due to the small number of spring/ summer-only feeders. A significantly higher proportion of those feeding year-round provisioned daily compared with autumn/winter-only households (test of two proportions; p = 0.0182) but overall feeding frequency was not significantly different, albeit marginally (Fisher's exact test; p = 0.061). Ninety-one per cent of feeding households gave between one and three types of food, with just two providing over five (Fig. 2).

We compared the percentages of respondents (using n = 499 as four gave only their parish/ ward) in different ACORN categories with those for SE England (see Appendix 1 for values and
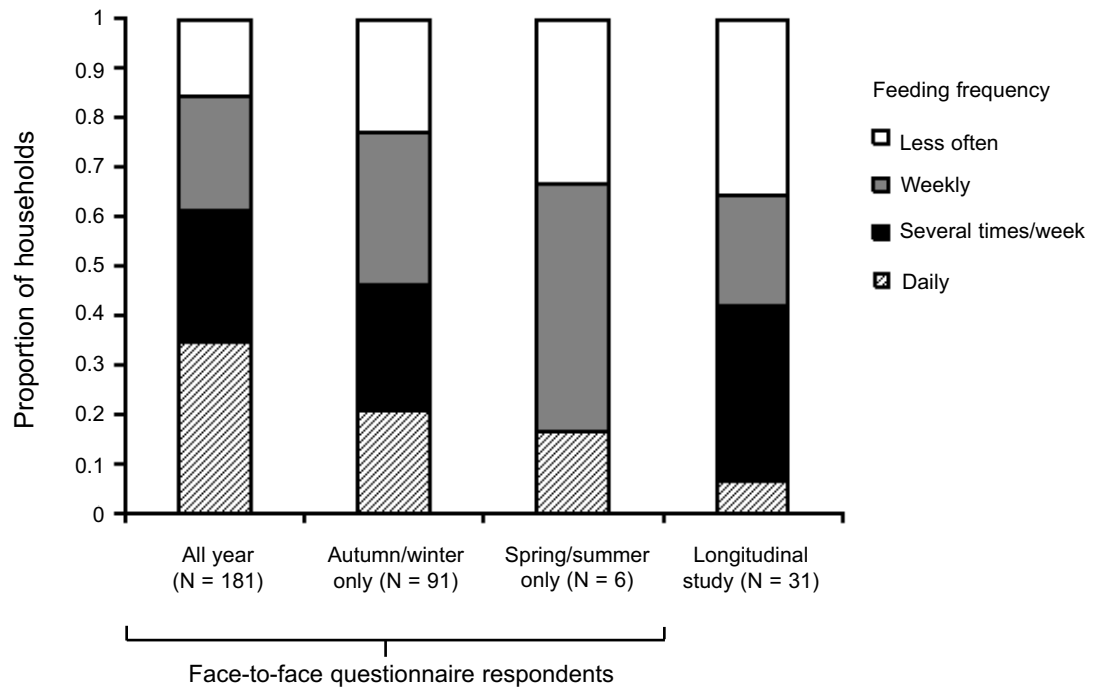
Fig. 1. Frequency of food provisioning for wild birds in Greater Reading, UK by participants in a one-off face-to-face questionnaire and a 2-year longitudinal study.

category descriptions). Although the percentages showed some differences in two of the five categories we considered our sample representative for the present purposes (see Appendix 1 for details). As a precaution, we recalculated the numbers feeding using correction factors for each ACORN category (SE England percentage/survey percentage). This increased the percentage of feeders slightly, to 56.9% (data not shown), but the difference between the raw and adjusted figures was not statistically significant (test of two proportions p = 0.610). We therefore used the unadjusted value in subsequent calculations.

Longitudinal bird-feeding study
Participant number varied amongst seasons (mean = 23, range = 20–27; unique households = 31; Table 1). Over the two years, the grand total of food was 4776 kg, equivalent to 19 097 845 kcal (see Table 1 for values by season) and UK £13 233 (November 2014 prices). The median given daily was 127 g/garden/day (range = 18–3573; interquartile range Q1–Q3 = 48–325) in mass, which provided 628 kcal/garden/day (range = 101–5872; Q1–Q3 = 262–912) in energy at an estimated cost of UK £0.35/garden/day (range = 0.05–9.90; Q1–Q3 = 0.13–0.90). The number of food
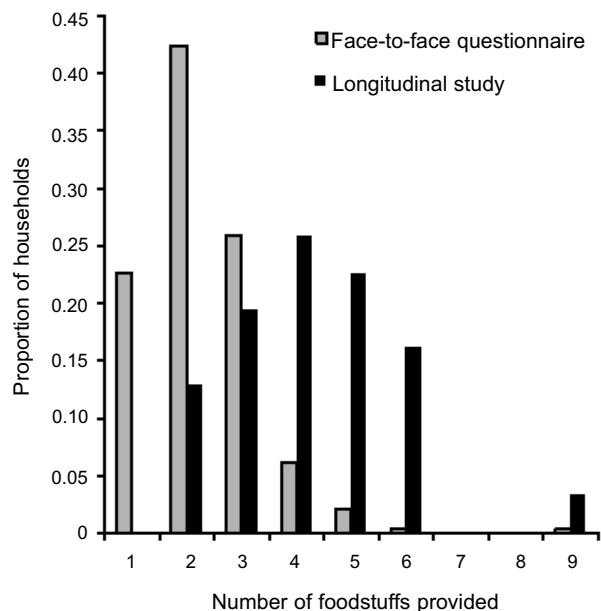

Fig. 2. Number of foodstuffs provided by bird-feeding households in Greater Reading, UK, taking part in a face-to-face questionnaire (n = 278) and a 2-year longitudinal study recording all food provided (n = 31; mean across seasons to nearest integer).

Table 1. Number of participants and total masses (kg) and kilocalories (kcal) of food provided for wild birds per season in a 2-year longitudinal study in Greater Reading, UK. Mean daily temperature and rainfall records for the area are also provided (data from University of Reading Atmospheric Observatory). *— Participation varied amongst seasons such that the total number of unique households was 31. [a] — Nine participants joined half-way through the first season and so these data were doubled.

Season	N households*	Total mass (kg)	Total kcal	Mean daily temperature (°C)	Mean daily rainfall (mm)
June−Aug 2010[a]	25	632.806	2 600 711	16.67	1.91
Sept−Nov 2010	27	551.120	2 381 919	10.23	1.67
Dec 2010−Feb 2011	25	623.197	2 491 496	4.05	1.75
Mar-May 2011	23	635.040	2 528 460	10.97	0.50
June−Aug 2011	22	703.151	2 803 793	15.67	2.00
Sept−Nov 2011	22	416.873	1 694 261	12.63	1.08
Dec 2011−Feb 2012	23	595.827	2 355 136	5.50	1.48
Mar−May 2012	20	617.552	2 242 069	9.67	2.02

categories provided varied amongst households (median = 4; Q1–Q3 = 3–5; n = 31; Fig. 2), as did feeding frequency (Fig. 1). Fifteen categories of food were provided across the two years (Fig. 3). Mixed seed was by far the most common by both mass and kilocalories (Fig. 3A, B, respectively). The potential for over-estimation of the amount of energy provided by low-calorie foodstuffs (see Methods) is clearly illustrated by the differing positions of fresh fruit in Figs 3A and B (both sorted in descending order). We therefore present only kilocalorific data for mean provisioning of the five most popular food categories per participant (Fig. 3C). The quantities of these varied by season (Fig. 3C) as did the proportion of households providing them across all categories (Appendix 3), with mixed seed again the most popular by both measures.

Given that study year and season were investigated in the linear mixed-effect modelling to examine seasonal variation in provisioning, we included only those households that participated in all seasons (n = 15) in this analysis. Model simplification revealed that none of the fixed explanatory variables (mean daily temperature and rainfall, season and study year) had a significant effect on the kilocalories provided (data not shown). One household was exceptionally prolific (upper outlier in Fig. 4 in all seasons) but was retained in the analysis as the $\log_{10}$-transformed kcal values were normally distributed for all seasons (untransformed values remained non-normally distributed with this household excluded).

Comparisons between data sets
The numbers of foodstuffs differed between the face-to-face questionnaire and longitudinal study participants (Fig. 2; medians of 2 and 4, respective-

ly). Comparison of daily, several times a week, weekly and less often provisioning between the data sets indicated significantly less frequent provisioning amongst the longitudinal study households (Fig. 1; Fisher's exact test p = 0.0073). The difference was more marked when only year-round feeders from the face-to-face questionnaire were considered (Fisher's exact test p = 0.0018). A similar result was found for at least weekly and less than weekly feeding (test of two proportions: p = 0.0119, 0.0079 using all feeders and year-round only from face-to-face questionnaire, respectively).

Estimated numbers of individuals supported
We provide the estimated numbers of individuals of the 10 species most commonly seen in UK bird-feeding gardens (see Methods) and of Grey Squirrels that could potentially be fully supported each day by the food provided by the longitudinal study participants in Table 2. We also provide extrapolations to Greater Reading and the whole of the UK for reference. The values assume 100% uptake of all resources by that species alone. However, our calculations for our average garden-feeding species (defined above) give an indication of the number of individuals that could be supported each day given a mixture of the 10 most common species — 15.4 individuals by the median provisioning level (range 3–149).

DISCUSSION

Face-to-face questionnaires
Just over half of the 503 Greater Reading households (55.3%) surveyed fed wild birds, a level broadly similar to nationwide estimates for the
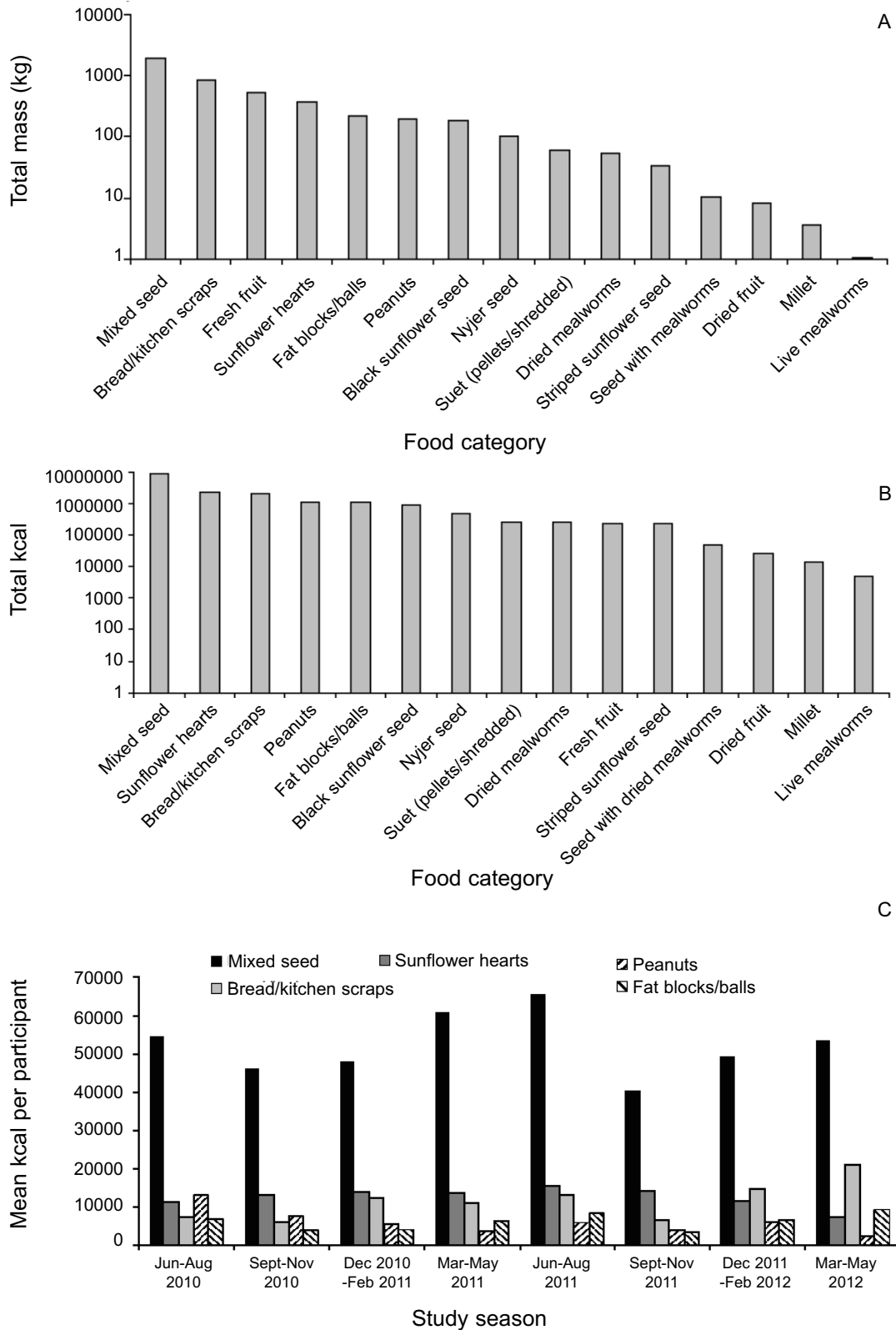
Fig. 3. Details of foods provided in a 2-year longitudinal bird-feeding study in Greater Reading, UK. A — Total mass (kg) and B — kilocalories (kcal) of each food category in descending order (note logarithmic scale), C — Mean kcal per participant for the five most provided food categories (by kcal). Both the number of participants and number providing each food varied amongst seasons (Table 1, Appendix 3). Nine participants joined half-way through the first season and so these data were doubled.

Fig. 4. Kilocalories (kcal) of wild bird food provided per household in a 2-year longitudinal study in Greater Reading, UK. Participant number ranged from 20–27 amongst seasons (mean = 23; Table 1). Nine joined half-way through the first season and therefore these data were 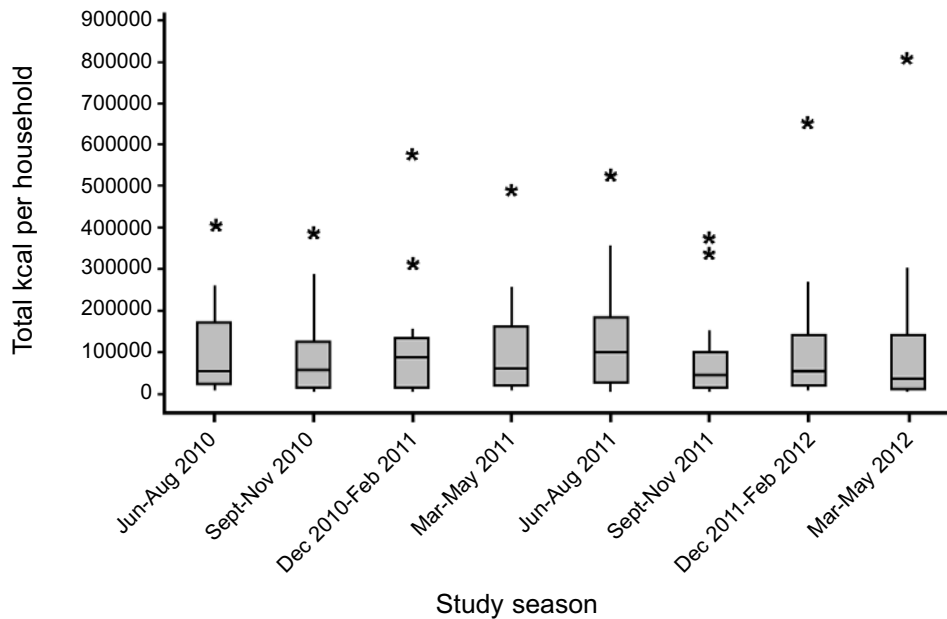doubled. Upper and lower limits of boxes = interquartile range; line within each box = median; upper and lower whiskers =upper and lower 25% of distribution, respectively, excluding outliers; * = outliers (greater than 1.5 × interquartile range above upper quartile).

UK, USA and Australia. Looking at other urban regions, in suburban and urban Michigan, USA, approximately two-thirds of households fed wild birds (Lepczyk et al. 2012), whereas across five UK cities, the level was lower, at 46.3% (Davies et al. 2012: figures recalculated to include households without access to outside space).

Two-thirds of the bird-feeding households fed year-round. This is lower than recent estimates elsewhere; for example, in suburban Brisbane, Australia, over 92% of households that fed wildlife did so (20/22 species were birds; Rollinson et al. 2003). However, in an earlier UK study, Cowie & Hinsley (1988) found that although around three-quarters of households fed birds (at least weekly) in suburban Wales, only 40% did so in summer. This suggests a shift in UK garden avian provisioning patterns over the last 25 years in line with advice from organisations such as the RSPB and BTO (Buczacki 2007). Furthermore, 82% of our participants fed at least weekly at the times of year when they fed, similar to levels recorded in Queensland, Australia (Ishigame & Baxter 2007). As an indication of the temporal reliability of supplementary provisioning at a landscape scale in Greater Reading, these figures correspond to 45%

of all households feeding birds at least weekly (i.e. including non-feeding households). This is almost identical to findings from urban Arizona, USA (43%; Lepczyk et al. 2012), but other UK results vary: Cowie & Hinsley's (1988) results mentioned above are substantially higher whereas the level was 29% across the UK cities surveyed by Davies et al. (2012).

Cowie & Hinsley's (1988) higher levels of at least weekly provisioning may at least partly reflect their relatively affluent suburban study area. Participation in bird feeding has been shown to correlate negatively with levels of socioeconomic deprivation in the UK (Fuller et al. 2008). However, we were intrigued by the generally greater levels of bird feeding, both in participation and feeding frequency, recorded here for Greater Reading compared with Davies et al. (2012). Both are recent studies of UK urban areas with broad socioeconomic coverage and bias due to interest in the subject minimised [our participants were unaware of the topic and Davies et al.'s (2012) data originated from a broad survey (CityForm) with few questions on bird feeding]. Given these similarities, we examined whether the different geographical scales might be a factor as

substantial regional variation has been recorded amongst English counties (Fuller et al. 2012) and US regions (Lepczyk et al. 2012). Indeed, the percentages of feeding households varied between 34 and 51% amongst the CityForm cities (supplementary appendix C in Davies et al. 2009, also CityForm data). Although CityForm selected specific inner, middle and outer areas to encompass the range of urbanisation and therefore city-wide provisioning levels may differ, the upper value (closest to ours for Greater Reading) was recorded in Oxford, just ~30 km away. This suggests that the difference between our figure and the combined CityForm value may indeed relate to regional variation in bird feeding.

Longitudinal bird-feeding study

Participants provided a median of four categories of food, compared with two in the face-to-face questionnaire and three and two in Michigan and Arizona, USA, respectively (Lepczyk et al. 2012). It is unclear whether this reflects a true difference in provisioning. Looking at specific foods, despite some differences in food types as expected by the differences amongst both avifaunas and climates, mixed seed was the most popular both here by all measures used (Fig. 3; Appendix 3) and in Michigan and Arizona (by proportion of feeding households; Lepczyk et al. 2012), and third in the wildlife-feeding study in Brisbane mentioned above (Rollinson et al. 2003). This may at least in

Table 2. Estimated numbers of birds and Grey Squirrels potentially supported by the median and lowest kilocalories (628 and 101 kcal, respectively) provided per household in a 2-year bird-feeding study, with extrapolations to Greater Reading and the whole UK. 100% uptake of resources assumed. Bird species are (in descending order) those recorded by the highest percentage of BTO Garden Bird Feeding Survey (GBFS) participants in winter 2012/13 (BTO 2013). The average feeding bird's requirements were calculated from the mean of the kcal requirements of these species with correction factors for the percentage of GBFS gardens in which they were recorded. * — Sources: Robin, Blackbird, Dunnock — Bryant 1997; Great, Blue and Coal Tits — Gibb 1957; Chaffinch — Cramp et al. 1994; Greenfinch, Woodpigeon — Christensen et al. 1996; Collared Dove — Cramp 1985; Grey Squirrel — Harris & Yalden 2008. Kilojoules were converted to kcal. Values are kcal consumed rather than used and thus were not adjusted for assimilation efficiency. Estimates are for wild animals except Gibb (1957), which are from outdoor aviaries. [a]— Percentage of households feeding in Greater Reading from present study; in UK from Davies et al. (2009); households from Office for National Statistics (2013), [b]— Median kcal per participant (N = 31, not all participated in every season). Nine participants joined half-way through the first season and so these data were doubled.

Species	Daily kcal*	Longitudinal study (per household)		Individuals supported daily: Greater Reading (55%, N = 53 090)[a]		UK (48% N = 12 692 206)[a]	
		Median kcal[b]	Lowest kcal	Median kcal[b]	Lowest kcal	Median kcal[b]	Lowest kcal
European Robin							
Erithacus rubecula	15	41.8	6.7	2 222 700	357 470	531 380 360	85 460 850
Blackbird							
Turdus merula	43	14.6	2.3	775 360	124 700	185 365 240	29 811 930
Blue Tit							
Cyanistes caeruleus	14	44.9	7.2	2 381 470	383 010	569 336 100	91 565 200
Great Tit							
Parus major	25	25.1	4.0	1 333 620	214 480	318 828 220	51 276 510
Chaffinch							
Fringilla coelebs	33	19.0	3.1	1 010 320	162 490	241 536 530	38 845 840
Dunnock							
Prunella modularis	21	29.9	4.8	1 587 640	255 340	379 557 400	61 043 470
Coal Tit							
Periparus ater	14	44.9	7.2	2 381 470	383 010	569 336 100	91 565 200
Greenfinch							
Chloris chloris	42	15.0	2.4	793 820	127 670	189 778 700	30 521 730
Woodpigeon							
Columba palumbus	160	3.9	0.6	208 380	33 510	49 816 910	8 011 960
Collared Dove							
Streptopelia decaocto	80	7.9	1.3	416 760	67 030	99 633 820	16 023 910
Average feeding bird	39.4	15.4	2.5	819 180	131 750	195 840 430	31 496 630
Grey Squirrel							
Sciurus carolinensis	137	4.6	0.7	243 360	39 140	58 180 330	9 357 030

part reflect the very wide availability of this food type for purchase (e.g. available in grocery stores and supermarkets as well as specialist retailers; Appendix 2; M. Orros, pers. observ.) compared with more specialised foods such as nyjer seed (typically only available from specialist retailers). Bread provision was also comparable between our participants (43%, our category included kitchen scraps) and Michigan and Arizona (32 and 47%, respectively; Lepczyk et al. 2012), although higher levels were seen in Brisbane (58%; Rollinson et al. 2003). However, in Cowie & Hinsley's (1988) earlier UK study, 90% of the bird-feeding households provided bread, the difference perhaps associated with the increase in both availability and variety of specialist foodstuffs as well as in advice on feeding in the UK in the intervening period (Toms 2003, Buczacki 2007).

Examination of numbers of foodstuffs and levels of popularity of different foods may underestimate the variety available to individual birds at the amongst-garden scale. The foods given varied amongst gardens providing similar numbers of categories here (data not shown), and further, the overall range was broader than that in any one garden (Figs 2, 3). Such variety, both within and amongst gardens, is relevant in the context of recent evidence of negative effects of provisioning dependent upon food type: wild Blue Tits *Cyanistes caeruleus* had impaired egg production when provisioned over winter only with fat but not with fat supplemented with vitamin E at the level found in peanuts (Plummer et al. 2013a).

Our data also indicate that differing results can be obtained when measuring provisioning by masses and kilocalories for foods of differing calorific values per unit mass (compare Fig. 3A and B). For example, fresh fruit scored far higher by mass than by kilocalories. This should be borne in mind for future quantitative studies of this kind.

Seasonal temperature, rainfall, study year and season had no significant effects on provisioning level. Considering that participants chose to fed birds year-round this is perhaps unsurprising. However, we acknowledge that our scale of measurement for temperature and rainfall (means over each 3-month study season) may be too coarse to detect differences in provisioning given the much finer timescale over which households would make such decisions. The small sample size for this analysis also clearly limited its statistical power but there was also no obvious seasonal

trend when all participants are considered (Fig. 4). Consistent with our findings, Cowie & Hinsley (1988) found no significant difference in the frequency at which households fed during winter and summer (although this included seasonal and year-round feeders).

Our estimated median daily cost of provisioning (UK £0.35) is equivalent to around UK £10 per month. We acknowledge that prices of wild bird food can vary considerably depending upon the quantity purchased, the retailer selected and any 'special offers' at the time of purchase (authors' pers. observ.; see also www.birdfood.co.uk for per-kg variation for different quantities and Appendix 2 for our selection method). The median cost may appear low to some keen bird-feeding readers; however, we recorded substantial amongst-household variation in provisioning (Fig. 4) with the upper quartile range value (UK £0.90) equivalent to ~UK £27 a month. We note that the estimated costs for the most prolific feeder (UK £9.90/day, 300/month) are an over-estimation as the great majority of food provided by this participant (by mass) was bread or fresh fruit, both relatively cheap foods (Appendix 2, the participant also informed us that much was purchased when reduced in price at the end of the day).

Comparisons between data sets

Before examining the numbers of individuals potentially supported by our longitudinal study participants, we considered how these households compare with the broader bird-feeding population. The median numbers of foodstuffs provided and the distributions differ (see Fig. 2) in a manner suggestive of greater provisioning amongst the longitudinal study group. In terms of feeding frequency however, provisioning was significantly less frequent in the longitudinal study. Given that their self-selection and generally higher number of food categories are suggestive of above-average provisioning levels, this raises the possibility that those surveyed face-to-face overestimated their provisioning rates. This possibility has implications for previous estimates of frequency derived from one-off questionnaires (e.g. Ishigame & Baxter 2007, Davies et al. 2012).

Estimated numbers of individuals supported

Our estimates of the numbers of individuals supported by garden bird feeding (Table 2) rest on the following assumptions in addition to that of 100%

uptake of the food provided: (1) that the energy requirement estimates used are representative (individual needs vary with various factors including size, ambient temperature and exertion levels — e.g. Goldstein 1988, Carey 1996, Bryant 1997); (2) that individuals are fully supported (to our knowledge 100% dependency of any wild bird population on supplementary provisioning has not been recorded: see Jones & Reynolds 2008); (3) that all food provided was equally available to all species irrespective of dietary requirements or dominance hierarchies (Sasvári 1988, Suhonen et al. 1992).

Taking these points and the representativeness of our sample as discussed above into account, we stress that the estimates in Table 2 are intended only as approximations that give some indication of the level of support deliberately made available to wild animals (target and non-target species) by domestic households. However, we believe that they are a useful step towards more precise quantifications of resource provision at regional and international scales that in our opinion are necessary in order to begin to interpret the implications of garden feeding of wild birds.

For comparison with our extrapolated numbers supported across the UK (Table 2), the total number of UK breeding individuals of the 10 species examined here was an estimated 71.1 million in 2009 (twice the breeding pairs in Eaton et al. 2012). Again, this is intended only as a rough comparison: many more species use supplementary foods in the UK (Chamberlain et al. 2005) as do non-breeding individuals of the species given here. Furthermore, the proportion of breeding individuals using gardens is likely to vary amongst species; national population and garden trends are not correlated for many species (Chamberlain et al. 2005).

Looking to other taxa, if Grey Squirrels took just 10% of the available resources recorded here, ~1 million individuals could be fully supported at the lowest support estimates, a significant proportion of the national population (most recent estimate of British prebreeding numbers — 2.5 million plus, Harris et al. 1995). Future work to determine the relative levels of support provided to target and non-target taxa would be of value.

CONCLUSIONS

We have provided the first quantitative estimates of the masses, kilocalories and costs of wild bird feeding in domestic gardens worldwide, and the first UK data on the seasonality of feeding and the types of food provided by households in over 25 years. These data have broad relevance beyond the supplementary provisioning of wild animals, with potential applications in fields such as urban ecology and socioeconomics.

Overall, our work indicates that supplementary provisioning in domestic gardens across the highly urbanised conurbation of Greater Reading is a widespread and temporally reliable resource for wild birds. This is consistent with previous findings of substantial provisioning in many countries and the activity's status as one of the most popular forms of human–wildlife interaction (Fuller & Irvine 2010). Even the lowest level of provisioning recorded is sufficient to fully support considerable numbers of individuals at a national level. Further research is required to estimate more precisely the extent to which birds are supported given that complete dependency appears unlikely and that the proportion of food taken by non-avian taxa remains unknown.

It is clear that the quantity of energy being added to garden ecosystems is vast and we urge further research into the consequences, particularly in the light of recent evidence of negative effects on birds including reduced productivity and impaired egg production (e.g. Harrison et al. 2010, Plummer et al. 2013a,b) and indirect negative effects on other taxa in the form of depletion of arthropod prey around garden feeders (Orros & Fellowes 2012, Orros et al. 2015). Furthermore, whether or not the end consumers are the intended targets, these individuals are receiving considerable additional energy and are thus being directly influenced in a way that species that do not take supplementary food, or do so to a lesser extent, are not. This is relevant to concerns over introduced, invasive species making use of supplementary foods such as the Ring-necked Parakeet *Psittacula krameri* in Europe (Strubbe 2009, Peck et al. 2014) and the House Sparrow *Passer domesticus* in North America and Australia (Jones & Reynolds 2008), or of behaviourally dominant species such as corvids that may outcompete smaller passerines for resources including food (Toms 2003, Jones & Reynolds 2008). The implications of these effects on community assemblages are as yet largely unknown. Overall, many fruitful avenues of investigation into this massive worldwide supplementary feeding experiment (sensu Jones & Reynolds 2008) remain.

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STRESZCZENIE

[Dokarmianie dzikich ptaków w ogrodach przydomowych w Wielkiej Brytanii]

Dokarmianie dzikich ptaków w ogrodach przydomowych jest bardzo popularne na całym świecie, zaangażowana w to jest około połowa gospodarstw domowych w Wielkiej Brytanii, Ameryce Północnej i Australii. Niemniej jednak, istnieje zaskakująco mało dokładnych danych o wielu aspektach takich działań podejmowanych przez mieszkańców.

W pracy na dwa sposoby scharakteryzowano dokarmianie ptaków w ogrodach przydomowych w obrębie dużej aglomeracji miejskiej (miasto Reading wraz z okolicznymi terenami) w południowej Anglii. Po pierwsze przeprowadzono badania ankietowe przed 10 supermarketami, obejmując dużą i reprezentatywną pod względem socjologicznym grupę mieszkańców (apendyks 1). Po drugie przeprowadzono szczegółowe badania, w których dokarmiający zapisywali częstość, rodzaj i ilość wykładanego ptakom dodatkowego pokarmu. W ten sposób uzyskano pierwsze całoroczne dane ilościowe dotyczące częstotliwości karmienia i rodzajów pokarmu, co pozwoliło na wyliczenia wartości energetycznej dostarczanego pokarmu. Analizy oparto na 503 odpowiedziach na pytania ankietowe oraz szczegółowych danych zbieranych przez dwa lata w 31 różnych gospodarstwach domowych. Jako, że dostarczany pokarm różnił się wartościami energetycznymi (apendyks 2), autorzy wyniki opracowali podając zarówno jego masę jak i wartość kaloryczną. Dokładny opis rodzajów pokarmu pozwolił także na opracowanie kosztów ponoszonych przez dokarmiających (apendyks 2).

Wyniki uzyskane z ankiet wskazują, że w ponad połowie gospodarstw domowych dokarmiane są ptaki, większość dostarcza dodatkowy pokarm przez cały rok, co najmniej raz w tygodniu (Fig. 1). Dane uzyskane ze szczegółowych obserwacji wskazują, że dziennie gospodarstwo domowe, w którym dokarmiane są ptaki dostarcza 127 g różnego rodzaju pokarmów, o wartości energetycznej 628 kcal (Tab. 1, Fig. 4).

Poszczególne gospodarstwa karmiły ptaki naj-częściej 3–5 rodzajami pokarmu (Fig. 2), łącznie do dokarmiania wykorzystywano 15 rodzajów pokarmu, wśród których największe znaczenie miały mieszanki nasion (Fig. 3, Apendyks 3). Szacunkowe koszty dokarmiania uzyskane na podstawie proporcji każdego rodzaju pokarmu w dostarczanym ptakom pożywieniu (apendyks 2) to 0,35 funtów szterlingów dziennie na gospo-darstwo domowe.

Nie stwierdzono, aby pogoda (średnia dzienna temperatura i średnia ilość opadów) lub sezon wpływały na łączną wartość energetyczną dostar-czanego pokarmu (Tab. 1). Porównanie pomiędzy danymi uzyskanymi dwiema metodami wykazało znacznie rzadsze dokarmianie wśród mieszkań-ców zaangażowanych w dokładne badania (zakładając jednocześnie większą chęć dokarmia-nia wśród tej grupy badanych) niż respondentów ankiet (Fig. 1), co sugeruje, że szacunki doty-czące częstotliwości karmienia ptaków uzyskane z danych ankietowych mogą być zawyżone.

Autorzy powiązali także wartość energetyczną dostarczanego dodatkowego pokarmu z zapotrze-bowaniem pokarmowym ptaków, uwzględniając 10 najczęściej spotykanych w ogrodach przydo-mowych gatunków ptaków, oraz wiewiórkę szarą, także często korzystającą z karmników (Tab. 2). Zakładając 100% wykorzystanie dostarczanego pokarmu, oraz uwzględniając wartość energe-tyczną uzyskaną jako mediana dla dostarczanego dodatkowego pokarmu, autorzy oszacowali, że dokarmianie ptaków przez gospodarstwa domo-we w skali całej Wielkiej Brytanii wystarcza do wykarmienia 196 milionów ptaków występu-jących w ogrodach w Wielkiej Brytanii. Wynik ten powstał w oparciu o zapotrzebowanie na energię 10 gatunków ptaków najczęściej stwierdzanych w ogrodach przydomowych. Natomiast biorąc pod uwagę najmniejszą wartość energetyczną dodatkowego pokarmu (tj. 101 kcal/dzień) stwier-dzoną podczas badań, szacunkowo ok. 31 mln tych ptaków w całej Wielkiej Brytanii może być utrzymywane wyłącznie przez dodatkowe dokar-mianie. Liczby te autorzy porównują z całkowitą wielkością populacji lęgowych tych 10 gatunków ptaków —71 milionów osobników.

Appendix 1. Brief description of the aspects of the CACI ACORN geodemographic categories relevant to the present study (see CACI 2010 for full category descriptions) and the percentages of our face-to-face questionnaire respondents* in each category with the equivalent values for South-East England as a whole for comparison[a].

ACORN category	Description	Face-to-face questionnaire respondents (%)	SE England households (%)
Wealthy achievers	Affluent, well above average incomes. Typically middle-aged or retired but also families with children. Large, detached houses. Wealthy suburbs if in towns/cities.	32	34
Urban prosperity	Broad range of incomes; typically above average. Broad age range (includes students and recent graduates as well as senior managers). Wealthier, older members typically in large houses; younger/less affluent in flats or student houses. Typically larger towns/cities, relatively central locations compared to other categories.	15	10
Comfortably off	Broad category with range of ages. Typically semi-detached or detached houses. Typically suburban areas if in towns/cities.	31	31
Moderate means	Average to below average incomes. Most often families with children at home. Typically terraced housing.	9	13
Hard-pressed	Group with lowest income. Broad age range. Typically terraced or semidetached housing on estates·	13	12

*— 499 of the total of 503 questionnaire respondents as four gave only their parish/ward.
[a] — Note that the percentages of our respondents in the different ACORN categories are similar to those of SE England for 'wealthy achievers', 'comfortably off' and 'hard-pressed'. However, 'urban prosperity' is over-represented and 'moderate means' under-represented, and a G-test indicated significant variation overall (G = 17.781, df = 4, p = 0.001). However, Reading (65% Greater Reading households) has more 'urban prosperity' (31%) and fewer 'moderate means' (11%) residents than does SE England and we considered our sample representative for the present purposes.
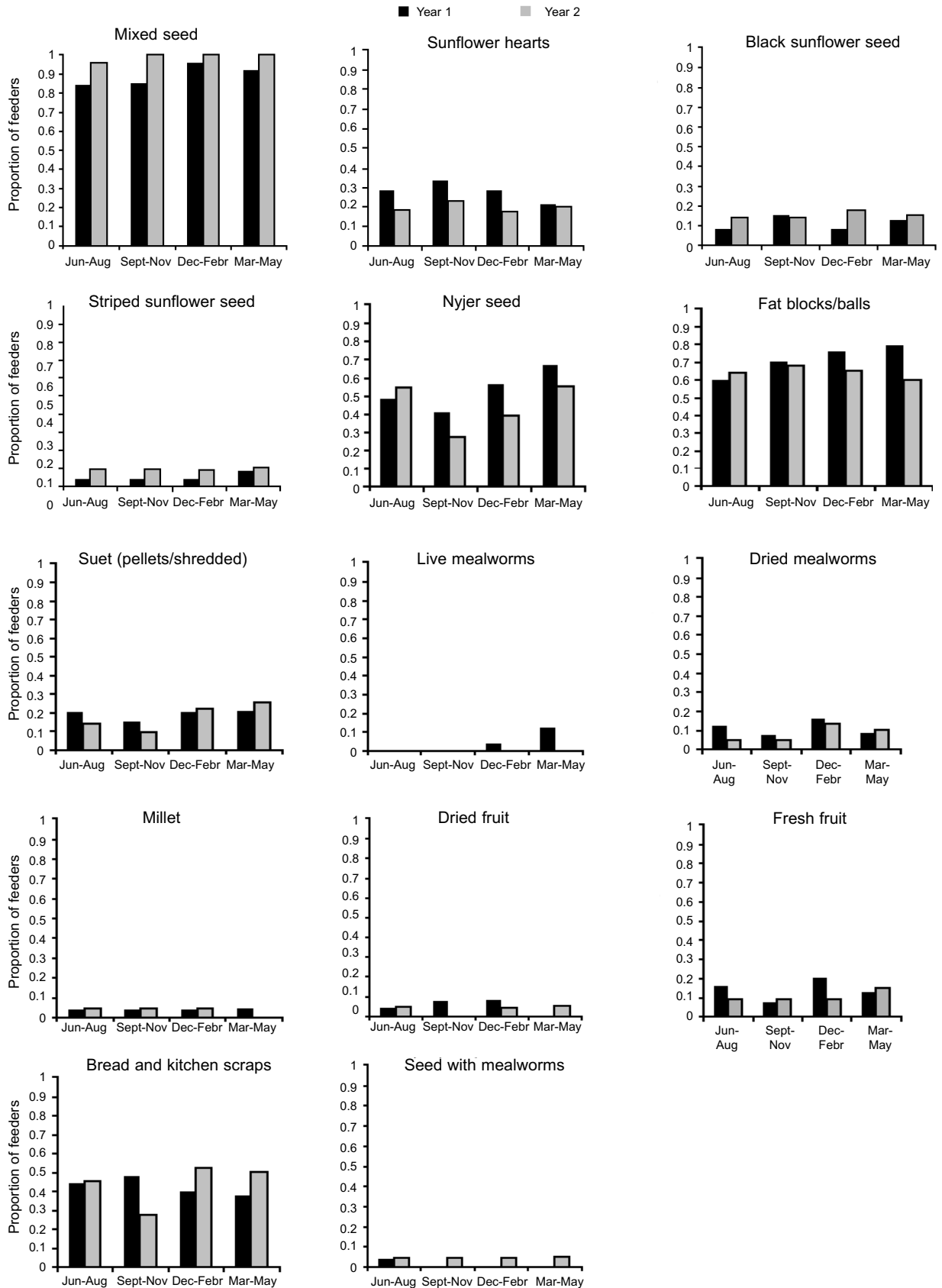
Appendix 2. Kilocalorific (kcal) values and costs (UK £ in November 2014) of supplementary foods provided for wild birds by participants in a 2-year study in Greater Reading, UK. Means are given for cases in which values of a single foodstuff differed amongst sources or for categories including a variety of similar food types (listed below table). Sources of kcal data: 1 — CJ Wild Bird Foods, www.birdfood.co.uk; 2 — RSPCA foods, sold via Tesco: http://www.tesco.com/groceries/; 3 — Tesco, http://www.tesco.com/groceries/; 4 — Exotic Nutrition Ltd, http://www.exoticnutrition.com/limein.html; 5 — http://www.calorie-counter.net/flour-calories/millet-raw.htm. Costs are the price of the food at Source 1 (the leading online bird food retailer in Europe) for all seeds/peanuts calculated from price for 2.5 kg bag (smallest bag available for all used in mean calculation for [a] below), 1 or 2 kg bag for suet pellets depending on size available, 100 g for live mealworms, 250 g for dried mealworms; at Source 3 (a major UK supermarket) for fresh fruit and bread/kitchen scraps (see [c] below), which were calculated from the price per kg and the price of a standard-sized loaf (800 g — Tesco own brand), respectively; at Vine House Farm (www.vinehousefarm.co.uk — retailer used by the participants providing this food) for millet ('white millet') calculated from price for 6 kg bag (not available at Sources 1 or 3).

Food category	Sources of kcal values	Kcal per 100 g	Cost (£) per 100 g
Mixed seed[a]	1, 2	476	0.34
Sunflower hearts	1, 2	620	0.27
Sunflower seeds (black and striped)	1	500	0.24
Peanuts	1	560	0.39
Nyjer seed	1	480	0.36
Seed with mealworms[b]	1	476	0.28
Suet blocks/balls[a]	1, 2	490	0.44
Suet pellets[a]	1, 2	438	0.62
Live mealworms	4	471	2.29
Dried mealworms	2	492	0.28
Millet	5	378	0.23
Dried fruit (sultanas taken as representative, as the only dried fruit sold by Source 1 as wild bird food)	1	310	0.64
Fresh fruit (apples and pears according to participants providing this food category).	3	46	0.17
Bread/kitchen scraps[c]	3	240	0.10

[a] — mixed seed includes: 'hi-energy supreme', 'hi-energy no mess', 'hi-energy seed', 'husk-free seed mix', 'robin blend', 'feeder seed', 'table seed', 'hi-energy ground blend', 'all seasons seed mix', 'every day seed' mix (all Source 1); 'RSPCA supreme feeder mix', 'RSPCA high energy no grow mix', 'RSPCA peanut-rich mix' (all Source 2). Suet blocks/balls and pellets include those also described as containing peanuts, mealworms, other insects and fruit (all Source 1).

[b] — Calorific value taken as that for mixed seed due to similarity between mixed seed and dried mealworm values and absence of data from Sources 1−3.

[c] — Brown, white and seeded bread taken as representative of this category. We acknowledge that calorific values of other scraps are likely to vary.

■ Year 1   ■ Year 2

Mixed seed

Sunflower hearts

Black sunflower seed

Striped sunflower seed

Nyjer seed

Fat blocks/balls

Suet (pellets/shredded)

Live mealworms

Dried mealworms

Millet

Dried fruit

Fresh fruit

Bread and kitchen scraps

Seed with mealworms

Appendix 3. Proportions of households providing each of 15 food categories in a 2-year longitudinal bird-feeding study in Greater Reading, UK.