Individual variation in winter supplementary food consumption and its consequences for reproduction in wild birds

Ross A. Crates*, Josh A. Firth*, Damien R. Farine, Colin J. Garroway, Lindall R. Kidd, Lucy M. Aplin, Reinder Radersma, Nicole D. Milligan, Bernhard Voelkl, Antica Culina, Brecht L. Verhelst, Camilla A. Hinde and Ben C. Sheldon

R. A. Crates (ross.crates@gmail.com), J. A. Firth, D. R. Farine, C. J. Garroway, L. R. Kidd, L. M. Aplin, R. Radersma, N. D. Milligan, B. Voelkl, A. Culina, B. L. Verhelst, C. A. Hinde and B. C. Sheldon, Edward Grey Inst. of Field Ornithology, Dept of Zoology, Univ. of Oxford, Oxford, OX1 3PS, UK.

The provision of wild birds with supplementary food has increased substantially over recent decades. While it is assumed that provisioning birds is beneficial, supplementary feeding can have detrimental 'carry-over' effects on reproductive traits. Due to difficulties in monitoring individual feeding behaviour, assessing how individuals within a population vary in their exploitation of supplementary food resources has been limited. Quantifying individual consumption of supplementary food is necessary to understand the operation of carry-over effects at the individual level. We used Radio Frequency Identification (RFID) technology and automated feeders to estimate individual consumption of supplementary winter food in a large wild population of great tits *Parus major* and blue tits *Cyanistes caeruleus*. Using these data, we identified demographic factors that explained individual variation in levels of supplementary food consumption. We also tested for carry-over effects of supplementary food consumption on recruitment, reproductive success and a measure of survival. Individual variation in consumption of supplementary food was explained by differences between species, ages, sexes and years. Individuals were consistent across time in their usage of supplementary resources. We found no strong evidence that the extent of supplementary food consumption directly influenced subsequent fitness parameters. Such effects may instead result from supplementary food influencing population demographics by enhancing the survival and subsequent breeding of less competitive individuals, which reduce average breeding parameters and increase density-dependent competition. Carry-over effects of supplementary feeding are not universal and may depend upon the temporal availability of the food provided. Our study demonstrates how RFID systems can be used to examine individual-level behaviour with minimal effects on fitness.

Over recent decades, the feeding of wild birds has increased in popularity in many areas and is now a multi-million dollar global industry (Jones and Reynolds 2008). However, only recently has attention been paid to the potential consequences of substantial supplementary feeding of wild birds. Since winter food availability is a major determinant of mortality and population regulation in seasonal temperate environments (Lack 1954), the widespread and reliable availability of food for wild birds may have effects at the individual level, and subsequently influence population-level demographics (Robb et al. 2008a). The consumption of non-natural food resources may alter the body condition of individuals in ways that affect their performance in the subsequent breeding season (i.e. 'carry-over effects' – Harrison et al. 2011). For instance, supplementary feeding may cause earlier egg laying and increased fledging success (Svensson and Nilsson 1995, Robb et al. 2008b), improved egg quality (Blount et al. 2002, Reynolds et al. 2003), increased clutch size (Rooney et al. 2015), survival (Brittingham and Temple 1988, Norris 1993) and reduced dispersal (Orell and Ojanen 1979).

Supplementary feeding may also have negative effects on reproduction. During the breeding season, supplementary feeding can lead to a reduction in average clutch and brood size in great tits and blue tits, and reduced hatching success in the latter (Harrison et al. 2010). Further, supplementary feeding during the winter can have carry-over effect on subsequent life-history stages. Plummer et al. (2013a) reported a reduction in reproductive success in blue tits supplemented over winter with fat, documenting reduced mean offspring weight, size and survival in comparison to

*Contributed equally to this work.

control populations. Thus, estimating the long-term effects of supplemental feeding of wild birds, and the mechanisms involved, is not straightforward.

Effects of food supplementation during the non-breeding season on reproductive traits could arise from either (or both) individual-level carry-over effects or effects on demography, e.g. by increasing overall survival rates. Whilst considerable variation may exist in the extent to which individuals within a population use supplementary resources (Robb et al. 2011, Bonter et al. 2013), most previous work has been limited to assuming individuals access supplementary food equally, due to difficulties in monitoring individual feeding behaviour (Harrison et al. 2010, Plummer et al. 2013a, b). Robb et al. (2011) found evidence of individual variation in supplementary food consumption using stable isotope analysis, but indirect techniques are limited in terms of the resolution that individual variation can be measured at. The classification of birds as supplemented versus non-supplemented in experimental and control treatments is likely to be a simplification, as many factors influence feeding patterns in wild birds. For example, dominance hierarchies during feeding affect the ability of willow tits *Poecile montanus* to gain mass during cold days (Koivula et al. 1995), while blue tits are subordinate to great tits in monopolising food resources and roosting sites (Dhont and Eyckerman 1980). Dominance hierarchies also exist with respect to age, sex and relative body size where older, male and larger-bodied individuals respectively, typically dominate each demographic class (Garnett 1981, Nilsson and Smith 1988, Sandell and Smith 1991). Dispersal status could also affect individual exploitation of supplementary food, due to dispersing (i.e. immigrant) birds being less competitive (Nilsson and Smith 1988) or having fewer social links to acquire information on food resource location in novel environments (Aplin et al. 2012).

In this study, we fitted Passive Integrated Transponder (hereafter 'PIT') tags to birds that could be detected by Radio Frequency Identification (hereafter 'RFID') antennae fitted to bird feeders. RFID technology enables standardised, contactless and non-invasive study of behaviour in wild animals. We used this approach to collect detailed, individual-level data on the feeding behaviour of a large population of blue and great tits supplemented through the winter with sunflower seeds. We estimated the individual consumption of seeds over the course of two years to address three aims. First, we quantified individual winter seed consumption levels, determined how consistent individuals were in their use of supplementary resources, and examined the relative importance of demographic factors in explaining the observed variation. Second, we tested for individual-level carry-over effects of winter supplementary feeding on subsequent life-history parameters, some of which have been assessed at the population level (Harrison et al. 2010, Plummer et al. 2013a, b). We examined whether winter seed consumption affected probability of recruitment, as well as of being observed in future – our best estimate of survival. For females that did breed, we assessed whether seed consumption had an effect on lay date, clutch size and egg mass. Finally, we looked for evidence of carry-over effects of seed consumption on later reproductive stages to consider potential carry-over effects in males as well as females via provisioning effort.

Material and methods

Seed consumption data

Data were gathered from a long-term study population of blue and great tits in Wytham Woods, Oxford, UK (51.7°N, 1.3°W), a 385 ha mixed deciduous woodland. Each individual was ringed with a standard BTO metal ring and fitted with a PIT tag (IB technology, Aylesbury, UK). It is estimated that 85–90% of great tits present in the woods were tagged during the study period (Aplin et al. 2014), although the proportion of blue tits tagged may be smaller. Tags were moulded into a split plastic colour ring with an internal diameter of 2.3 mm for blue tits and 2.6 mm for great tits. Sixty-five seed feeders were distributed in a grid throughout the site, at intervals of 250 m. Each feeder had 2 seed dispensing openings fitted with RFID antennae perches. Antennae remotely detected the RFID code of PIT tags fitted to individual birds that visited the feeder, recording these to a data logger. The detection range of each antenna was approximately 5 cm, meaning individuals were highly likely to only be recorded if they perched on the antennae to take a seed from the feeder.

During two consecutive winters (3 December 2011 to 27 February 2012 and 1 December 2012 to 3 March 2013), birds were provided with husked black sunflower seeds each Saturday and Sunday (Jacobi Jayne, Kent, UK). Mean monthly temperatures within the wood were similar across both winters and broadly in line with the long term average. December to February values were 4.8, 5.1 and 3.5°C in 2011/2012 and 4.6, 3.2 and 2.4°C in 2012/2013 (Environmental Change Network 2015). Feeders were programmed to automatically open pre-dawn and close post-dusk over the weekend, and were closed during weekdays. No birds could access supplementary food during this time and were therefore dependent upon foraging for natural foods within the wood, such as beech mast and invertebrates. While it is possible that some individuals may feed in adjacent gardens during the week, very few feeders are located within 1 km of the woodland edge. Since the birds in our study area are relatively sedentary during winter (Matechou et al. 2015), we are confident that the vast majority of birds were not exploiting alternative supplementary food resources during the week. The design of this study was part of a larger project investigating the winter behaviour of the wild tit community. Although providing intermittent access to supplementary food in this way should still allow assessment of the factors governing individual variation in supplementary food exploitation, it may reduce the extent to which the consequences of food exploitation (e.g. fitness) can be generalised to constant-provisioning scenarios. However, whilst some research has investigated the influence of constant provisioning (at least at the population level), the consequences of a less stringent feeding regime, which may be reasonably common under less standardized situations such as garden bird feeding, has not been investigated. Similarly, whilst some previous studies of supplementary feeding may have provided food every day, most have not quantified individual-level access to feeders, making it difficult to determine the consistency that birds actually accessed the supplementary food. Our study design also enabled us to assess whether

employing an RFID tracking system, which has many uses for studying avian ecology (reviewed by Bonter and Bridge 2011), based on supplying food to attract tagged individuals to RFID loggers over intermittent periods, can indirectly influence life-history variables.

Feeders logged each record of a bird at a frequency of 1/3 s, resulting in multiple records per bird per visit. We developed an algorithm that assessed the distribution of inter-visit intervals (the gap between two consecutive records) to infer the number of seeds taken. For each bird, the inter-visit intervals has a bimodal distribution, with a very large peak at ≤ 1 s, and a second peak at around 60 s. These peaks relate to within-visit intervals and between-visit detections respectively. This distribution occurs because birds typically visit a feeder to obtain a single seed, which they consume after flying into nearby vegetation (resulting in a temporal gap between each seed collected), but the RFID loggers record the presence of birds up to 3 times per second. To remove multiple records in the data that constitute a single visit, we identified the inter-visit interval corresponding to the lowest value between the two peaks in the distribution (i.e. the least common interval). We repeated this for each individual and calculated the 95% range of this value across all individuals combined (Fig. 1a). These values enabled us to assign visits to one of three categories (Fig. 1b): A) intervals that are part of the within-visit distribution of intervals, B) intervals that are uncertain (those that fell within the 95% range of minimum values), C) intervals that are part of the between-visit distribution of intervals. Interval 'B' ranged from 5 to 23 s in 2011/2012 and 5 to 24 s in 2012/2013, and accounted for 2.3% of the data in both years. Interval 'C' accounted for 29.1% of the data in 2012 (1 594 924 unique visits) and 27.9% of the data in 2013 (1 118 004 unique visits). We used the number of records for each bird with an inter-visit interval greater than 23 s in 2012 (which included 2567 individuals) and 24 s in 2013 (1964 individuals) as an estimate of the number of seeds consumed. We used R, ver. 3.1.2 (R Development Core Team) for all analyses. Thresholds used to calculate inter-visit intervals were almost identical for both species. The energetic content of the seeds we provisioned was estimated to be 1.05 kJ seeds^{-1} (average husked, dry weight energetic content = 19.9 kJ g^{-1}, average seed mass = 0.0528 g, J. Jayne pers. comm). Sunflower seeds are also high in protein (0.2 g g^{-1}) and vitamin E (0.35 mg g^{-1}, USDA 2007).

Reproductive data

Birds breeding in nest boxes throughout the woods were monitored from April to July, where 1 April was considered as day 1 for data analysis. Nests were monitored on a weekly basis until eggs were discovered within each active box. Where more than one egg was present in a nest, lay date was estimated by back-calculating from the day of observation, based on the assumption that blue and great tits lay one egg per day (Perrins 1996). Mean egg mass was calculated to the nearest 0.1 g by weighing a minimum of 3 eggs per clutch prior to incubation (Rahn and Ar 1974). Clutch size was recorded as the maximum number of eggs counted within the nest after commencement of incubation, unless a larger number of eggs or chicks were recorded during hatch checks. We recorded hatch date by visiting each nest every other day from the expected hatch date until hatching occurred.

Parents were identified in one of two ways. When chicks were aged between 7 and 11 d, the detachable front of each box was replaced with an identical front, to which an RFID antenna was attached around the entrance hole, powered by a concealed 9 V battery. If the parents were PIT tagged
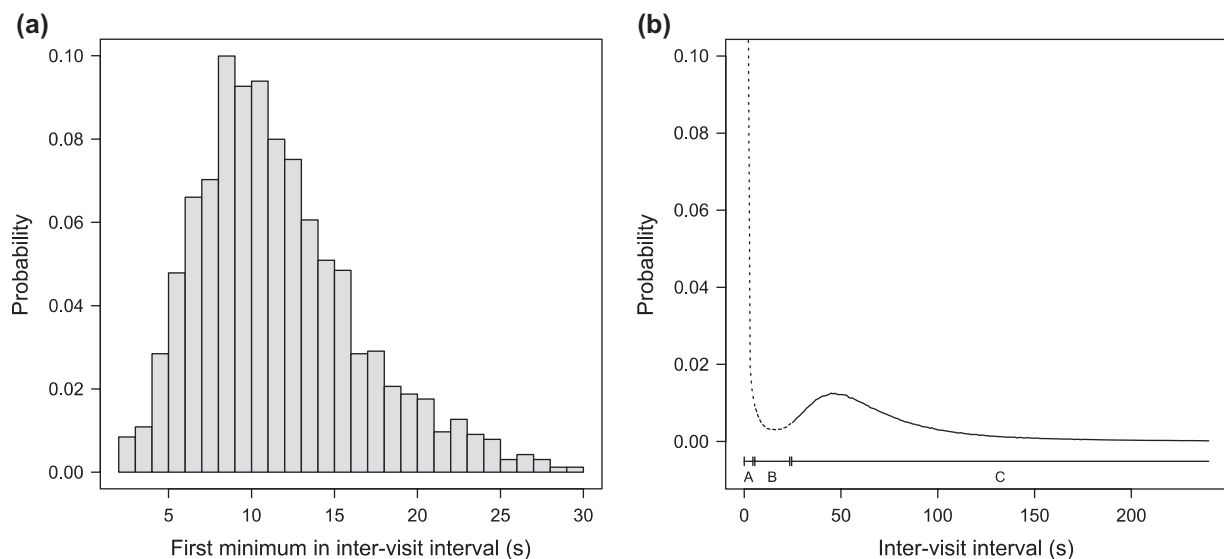

Figure 1. (a) Frequency distribution of the inter-visit interval corresponding to the minima between the two peaks in the distribution across all individuals and (b) probability distribution of inter-visit intervals for remotely-detected feeding data from a population of great tits (n = 1240) and blue tits (n = 1672) combined. The regions A to C in this graph identify intervals that correspond to the within-visit recording interval, intervals that cannot be allocated to within or between visit, and intervals correspond to between-visit intervals. Thus, only the occurrence of a gap between records that falls within the region of area C is used when estimating the number of seeds taken by each individual.

prior to breeding, their identities were remotely recorded as they entered the nest box to provision the chicks. The RFID fronting was left on each nest for a maximum of 1.5 h. If the fronting method failed to identify both parents, they were caught at the nest box using a spring-loaded trap when chicks were aged 11–15 d. Adults were ringed and tagged if unringed upon capture, and sexed by plumage traits and the presence of an incubation patch or a cloacal protuberance in females and males respectively (Svensson 1992). For breeding birds detected remotely, we inferred age and sex from previous breeding attempts or from the previous capture data of the partner. We also inferred the sex of great tits previously only captured outside of a breeding season based on plumage traits (Svensson 1992). Because blue tits cannot be sexed with certainty outside of the breeding season, remotely-detected blue tits that were not previously captured, or whose partner was not previously captured during a breeding season were left unsexed. All breeding birds were aged as adults (age > 1 yr) or first years, based on plumage traits (Svensson 1992).

We classified the dispersal status of each individual as local if they were originally ringed as a chick within the study site, or an immigrant if not (Table 1). While a small number of birds breed in natural cavities, estimates of recapture rates of tits in Wytham Woods suggest that the great majority of birds breed in boxes (Lachish et al. 2011, Kidd et al. 2015). In addition, we defined birds as 'winter residents' if they were observed on at least 10 out of 12 weekends each winter, representing all birds recorded on greater than the population median number of weekends (i.e. the right hand of the bimodal distribution – Supplementary material Appendix 1, Fig. A1). We classified birds as breeding recruits if they were detected at a nest box during the spring following the winter in focus.

All chicks were ringed and fitted with a PIT tag age 15 d (hatch = day 1), and weighed to an accuracy of 0.1 g. Fledge checks were conducted one week after the expected fledge date. We calculated fledging success as the number of young fledged divided by the clutch size of each box. Because oak tree *Quercus* sp. density within the territory of each nest box is known to be a predictor of reproductive success (Wilkin et al. 2009), we controlled for this in our analysis by counting the number of oak trees greater than 50 cm diameter at breast height within 75 m of each nest box.

Data analysis

Individual variation in supplementary food consumption

Considering each species separately, we examined how demographic characteristics; namely sex, age, and dispersal status affected individual seed consumption levels. Annual seed consumption was strongly related to the number of weekends that a bird was observed at the feeders. Therefore, using the demographic characteristics as explanatory variables, we fitted linear mixed models (LMMs) using the lme4 package (Bates et al. 2014), setting the estimated number of seeds each bird consumed each weekend as the response variable (which was normally distributed – Fig. 2) and including individual identity as a random term. This also enabled us to determine individual consistency in exploitation of supplementary food resources by calculating the total variation

that was accounted for within repeated measures of the same individual (Nakagawa and Schielzeth 2013). To account for differences between the two years, year was included as a categorical fixed effect. Similarly, as reliance on supplementary foods is likely to increase through the winter as weather conditions harshen, and individuals may differ in their temporal occurrence through the winter, we also included weekend number/ID as a numerical fixed effect to control for this. Initially, we conducted this analysis on winter residents only (see above; great tit n = 788, blue tit n = 814). Restricting the analysis to winter residents ensured that birds had access to the supplementary food resources throughout the majority of the winter and reduced the likelihood that these birds were exploiting supplementary food resources outside of the study area. However, as this may exclude some birds that occurred in the woodland but did not utilize the feeders regularly, we also ran the same models for two other sets of individuals. Firstly we considered only birds that were subsequently recorded breeding (great tit n = 568, blue tit n = 549). By considering breeding birds we were able to include 'distance from nest box to most frequently-visited feeder' as an explanatory variable to assess the influence of spatial location. Secondly, we also ran the analysis for all birds (including breeding and winter residency status as explanatory variables; great tit n = 1240, blue tit n = 1672), to broadly assess if using subsets of particular interest or considering certain types of individuals had any effect. For all LMMs, we assessed support for variables based on breadth and position of confidence intervals and effect sizes, as per Nakagawa and Cuthill (2007).

Carry-over effects on recruitment to the breeding population

We also examined how individual recruitment to the breeding population that year was influenced by supplementary food consumption. Using 'recruitment' as the binary response variable, we used generalized linear mixed models (GLMMs) with a binomial error structure to estimate the effect of estimated yearly seed consumption (square root transformed to aid model convergence), whilst accounting for sex, age, dispersal status and year. We also added individual identity as a random effect to account for repeated individuals between years. Initially, we restricted this analysis to winter residents (defined above) because transient birds may consume less seeds and to control for known effects of winter residency on recruitment (Farine and Sheldon 2015, Matechou et al. 2015). We repeated the analysis in two ways. Firstly we included the number of weekends each bird was recorded as a fixed effect, permitting an assessment of the effect of increased presence even within winter residents. Secondly, we included all individuals in the population, but instead of using total seeds consumed, we used the rate of estimated seed consumption as the predictor variable. Consumption rate was estimated by dividing individual total winter seed consumption by the number of weekends they were detected at a feeder. This allowed us to gain an understanding of the influence of considering a subset of particular interest in comparison to the whole population. As a supplementary analysis, we also ran the same models but setting the binary response variable as whether a bird was observed following the winter. This provides a best estimate of survival, but is

Table 1. Variables contained within models to explain variation in individual seed consumption levels in a population of great tits and blue tits, and to test for carry-over effects of seed consumption on survival and breeding parameters.

Fixed predictors	Description/levels	Justification	Models included as a variable							
			SC	R	S	LD	CS	EM	NM	FS
Annual seed consumption	Continuous factor, great tit range 1–2201, mean 815 ± 468; blue tit range 1–1859, mean 527 ± 425.	Test for potential negative effects of seed consumption on survival and recruitment.	✓	✓	✓	✓	✓	✓	✓	✓
Weekly seed consumption	Continuous factor, great tit range 1–240, mean 85 ± 37; blue tit range 1–213, mean 64 ± 37.	Test for potential negative effects of seed consumption on survival and recruitment.	✓							
Age	2-level factor, adult or first-year.	Age differences in seed consumption and age affects breeding parameters (Bouwhuis et al. 2009).	✓	✓	✓	✓	✓	✓	✓	✓
Sex	2-level factor, male or female.	Potential sex differences in seed consumption, and also in effects on breeding success.	✓	✓	✓					
Feeder distance	Linear distance from main feeder to breeding box. Continuous (to nearest 10 m), range 10–3350, mean 200.	Potential negative correlation between distance to main feeder and seed consumption.	✓			✓				
Weekends	Weekends an individual was detected (for yearly consumption) or the specific weekend detected (for weekly). Continuous, range 1–14.	Positive correlation between seed consumption and number of weekends observed at the feeder.	✓	✓	✓	✓	✓	✓	✓	✓
Box altitude	Continuous, range 60–166 m, mean 103 m.	Negative correlation between altitude and lay date, due to temperature decrease with altitude (Perrins 1970).				✓				
Dispersal status	2-Level factor, immigrant or resident.	Potential differential use of supplementary feeders between immigrants and residents, also differences in RS between the two groups (Nilsson and Smith 1988).	✓	✓	✓	✓				
Oak density	Number of mature oaks within 75 m of breeding box. Continuous, range 0–87.	Breeding success strongly linked to oak density in tits (Wilkin et al. 2009).					✓	✓	✓	✓
Lay date	Date of first egg, where 1 April = 1. Continuous, range 1–80 mean 17 (2012), 35 (2013).	Lay date affects clutch size, brood mass and fledging success (Norris 1993).						✓	✓	✓
Clutch size	Discrete count, great tit range 2–13, median 7; blue tit range 2–15, median 9.	Clutch size affects egg mass and brood mass (Perrins 1996).						✓	✓	
Year	2-level factor, 2012–2013.	Account for annual variation in seed consumption due to e.g. availability of natural food (Perrins 1966).	✓	✓	✓	✓	✓	✓	✓	✓
Random effects										
Individual	Multi-level factor. See results and SI for specifics of each model.	Test for individual consistencies in seed consumption across years and control for multiple observations of individuals across weekends and years.	✓	✓	✓	✓	✓	✓		
Box	Multi-level factor. See results and SI for specifics of each model.	Control for territory effects and use of boxes across both years.					✓	✓	✓	✓

Model abbreviations: SC, seed consumption; R, recruitment; S, survival; LD, lay date; CS, clutch size; EM, mean egg mass, NM, mean nestling mass; FS, fledging success. See Supplementary material Appendix 1, Table A1.1–A2.4 for further details of model construction.

difficult to disentangle from dispersal (see Supplementary material Appendix 1, Table A4.1–A4.2 for details).

Carry-over effects on reproductive success

For breeding birds of each species, we considered how yearly supplementary food consumption influenced various measures of reproductive success. We fitted LMMs separately for the response variables lay date, clutch size, mean egg mass, mean nestling mass and overall fledging success, including individual identity and nest box as random terms. For lay date, clutch size and mean egg mass, only maternal seed consumption was considered. For mean nestling mass and fledging success, paternal seed consumption was also included (which showed a 0.38 and 0.50 correlation with maternal seed consumption for blue tits and great tits respectively). Further details of fixed effects are outlined in Table 1. We repeated each model with a) number of weekends each bird was detected included as a fixed effect and b) considering
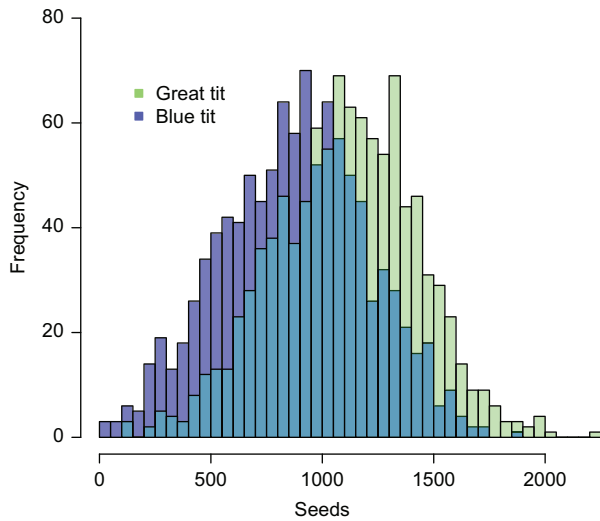
Figure 2. Frequency distribution of total estimated winter consumption of supplementary sunflower seeds in a winter resident population of great tits (green bars) and blue tits (blue bars). Turquoise (blend of blue and green) shows the smallest frequency of the two species when they overlap. Values are per bird per year, and only includes birds classed as winter residents of the study area (see Material and methods).

rate of seed consumption instead of total seed consumption. Known re-nesting attempts, which were rare (< 2%), were excluded from all analyses.

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.4ch2c> (Crates et al. 2016).

Results

Individual variation in supplementary seed consumption

There was substantial variation in the extent to which birds within the population consumed seed from the supplementary feeders. In general, great tits consumed significantly more seeds (ca 35%) than blue tits (Fig. 3, Table 1). Considering the winter residents, the mean estimated annual seed consumption ($\pm$ SD) in great tits was 1102 $\pm$ 323 (range 115 to 2201) and in blue tits was 876 $\pm$ 328 (range 15 to 1859, Fig. 2). Estimated seed consumption per weekend across all birds averaged 91 $\pm$ 37 in great tits and 64 $\pm$ 37 in blue tits.

Our model of variation in seed consumption identified several demographic factors that each explained a significant proportion of the variation (Table 2). In the resident population, first year birds tended to consume more seeds than adults, though this difference was only significant in great tits (Table 2, Fig. 3). In both species, the greatest difference in levels of seed consumption was found between the sexes, with males consuming significantly more than females. Dispersal status had no effect on seed consumption (Table 2, Fig. 3). We also found that increasingly more seeds were taken over weekends later in the season (Table 2), in line with predictions that usage of
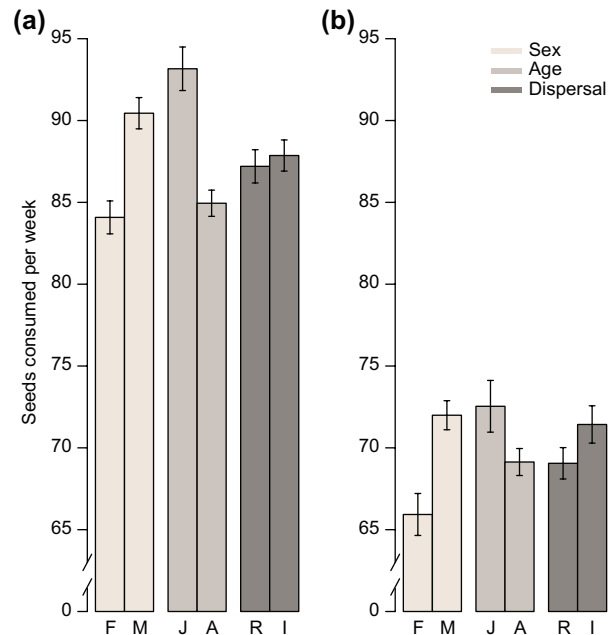

Figure 3. Variation in mean ($\pm$ SE) estimated weekly consumption of supplementary seeds (averaged for each individual) by sex, age and residency status in a wintering population of (a) great tits and (b) blue tits. X axis abbreviations for sex: female (F) and male (M); age: juvenile (J) and adult (A); and dispersal status: resident – i.e. locally-born (R) and immigrant (I). Values are calculated using only birds classed as winter residents of the study area (see Material and methods).

supplementary food may increase over the winter. Additional models that: a) restricted the analysis to breeding birds only and b) included the whole population, yielded very similar patterns (Supplementary material Appendix 1, Table A1.1 and A1.2). Individual consistency in the number of seeds consumed across observations (i.e. weekends) was reasonably high in both great tits (residents: r = 0.33, n = 788; breeders: r = 0.38, n = 568; overall: r = 0.41, n = 1240) and blue tits (residents: r = 0.39, n = 814; breeders: r = 0.47, n = 549; overall: r = 0.46, n = 1672). Individuals also showed similar levels of repeatability across weekends when each year was considered separately and also across years (Supplementary material Appendix 1, Table A2).

Carry-over effects on recruitment to the breeding population

For great tits, there was no evidence that seed consumption influenced recruitment to the breeding population of the winter residents (Table 3). This was also the case when including the number of weekends each bird was detected as a fixed effect in a model, or considering seed consumption rate of all individuals (not just winter residents) (Supplementary material Appendix 1, Table A3.––A3.2). The same result of no carry-over effects of seed consumption was found when an estimate of survival was considered instead of recruitment to the breeding population (Supplementary material Appendix 1, Table A4.––A4.3). Similarly, whilst a marginally significant (although

Table 2. Linear mixed model of factors affecting variation in estimated weekly winter supplementary seed consumption in a resident population of great tits and blue tits. Bold indicates the effects that are more than twice the standard error around the estimate.

	Great tit, n = 788			Blue tit, n = 814		
	Est.	SE	t	Est.	SE	t
Intercept	**78.608**	**1.558**	**50.454**	**56.471**	**1.699**	**33.241**
Age Relative to juveniles	**–8.795**	**1.135**	**–7.751**	–2.001	1.159	–1.726
Dispersal status Relative to immigrants	0.301	1.534	0.196	1.871	1.659	1.128
Sex Relative to females	**6.244**	**1.533**	**4.073**	**6.797**	**1.651**	**4.117**
Weekend Numerical from start of winter	**1.240**	**0.067**	**18.383**	**1.275**	**0.063**	**20.201**
Year Relative to 2013	**4.494**	**0.797**	**5.640**	0.043	0.755	0.057

not accounting for multiple testing) positive relationship was found between seed consumption and recruitment in winter resident blue tits, no evidence for carry-over effects was found when weekend occurrence was accounted for (Supplementary material Appendix 1, Table A3.1), or when considering seed consumption rate of all blue tits (Supplementary material Appendix 1, Table A3.2), as well as when considering survival (Supplementary material Appendix 1, Table A4.1–A4.3). When accounting for multiple tests on the data, no convincing evidence of carry-over effects of seed consumption onto recruitment (or estimated survival) was found within the population.

Carry-over effects on reproductive success

Estimated annual seed consumption in both sexes had no effect on any of the breeding parameters we tested in either species. Lay date increased with box altitude for both species. In great tits, adult and locally-born females started their clutches earlier than first-year and immigrant birds. In both species, there was a negative relationship between lay date and clutch size and in great tits there was a negative relationship between egg mass and clutch size. Clutch size was the key predictor of brood mass in both species and in great tits, there was a tendency for earlier hatched broods to be heavier. Mean nestling mass was the key predictor of fledging success for both species (Table 4). The same patterns were found when considering seed consumption rate, and when controlling for winter residency (Supplementary material Appendix 1, Table A5.1 and A5.2).

Discussion

Through the automated monitoring of individuals within a large community of wild birds, we identified factors that explained individual variation in the consumption of supplementary food resources. We then tested for individual-level carry-over effects of supplementary food consumption on a number of subsequent fitness parameters. There was substantial variation in the extent to which individuals exploited supplementary food resources and individuals were consistent in the degree to which they fed on supplementary food over both short (weekends) and long (years) time periods. Variation in supplementary food consumption was linked to a number of demographic traits at the individual level, but at this level, we found no evidence of carry-over effects of winter seed consumption on reproductive success. Our results suggest that negative effects of supplementary feeding demonstrated previously (Harrison et al. 2010, Plummer et al. 2013a, b) may have arisen through increased food availability influencing population demography, for example increasing the survival of low-quality individuals and potentially increasing resource competition during the breeding season. Additionally, temporally limiting the availability of supplementary food, as we did here, and which might occur in garden environments, may also prevent the development of carry-over effects.

Several factors predicted individual differences in supplementary food consumption. First-year birds consumed more seed than adults. Although adults may be expected to dominate younger birds for access to food resources, dominance

Table 3. Generalised linear mixed model of the effect of estimated total winter supplementary seed consumption on recruitment in a winter resident population of great tits and blue tits. p values reported are calculated under the default lme4 method (Bates et al. 2014).

	Great tit n = 788				Blue tit n = 814			
	Est.	SE	z	p	Est.	SE	z	p
Intercept	0.373	0.468	0.796	0.426	–1.698	0.423	–4.013	<0.001**
Age Relative to juveniles	0.046	0.153	0.297	0.766	–0.211	0.172	–1.228	0.219
Dispersal status Relative to immigrants	–0.217	0.138	–1.565	0.118	0.025	0.157	0.156	0.876
Sex Relative to females	–0.379	0.141	–2.684	0.007*	0.204	0.165	1.233	0.218
Seeds consumed	–0.002	0.014	–0.124	0.901	0.026	0.013	2.049	0.04*
Year Relative to 2013	–0.079	0.147	–0.535	0.593	0.022	0.147	0.148	0.883

Table 4. Summary of linear mixed models examining the effect of total estimated winter supplementary seed consumption on subsequent breeding success in a population of great tits and blue tits. Bold indicates the effects that are more than twice the standard error around the estimate.

Fixed effect	Lay date			Clutch size			Mean egg mass			Mean nestling mass			Fledging success		
	Est.	SE	t	Est.	SE	t	Est.	SE	t	Est.	SE	t	Est.	SE	t
Blue tit	n = 284			n = 284			n = 265			n = 167			n = 167		
Box altitude	**0.035**	**0.018**	**2.007**												
Mean brood mass										**−0.080**	**0.040**	**−1.986**	**6.814**	**2.106**	**3.236**
Clutch size										−0.208	0.148	−1.406	−4.006	4.001	−1.001
Female age	−1.509	1.005	−1.501	0.144	0.229	0.630	−0.003	0.003	−1.212						
Female dispersal status	1.394	0.929	1.501				0.010	0.012	0.854						
Distance from nest box to feeder	0.002	0.001	1.292				0.000	0.000	0.802						
Female annual seed consumption	0.000	0.001	−0.072	0.000	0.000	−0.583				0.000	0.000	−0.055	−0.001	0.005	−0.133
Lay date				−0.104	0.014	−7.392				0.009	0.010	0.843	−0.493	0.261	−1.889
Male age										−0.019	0.146	−0.128	1.341	3.915	0.343
Male annual seed consumption										0.000	0.000	**−2.182**	−0.004	0.005	−0.875
Oak density				0.008	0.007	1.050	0.000	0.000	−0.552	−0.002	0.004	−0.360	−0.068	0.118	−0.579
Year	**17.833**	**0.866**	**20.600**	**0.791**	**0.322**	**2.459**	**0.026**	**0.010**	**2.627**	0.355	0.224	1.587	**15.049**	**6.012**	**2.503**
Great tit	n = 358			n = 358			n = 327			n = 208			n = 208		
Box altitude	**0.043**	**0.016**	**2.791**												
Mean brood mass										**−0.221**	**0.083**	**−2.672**	**3.404**	**0.857**	**3.970**
Clutch size										−0.406	0.300	−1.353	5.057	3.698	1.367
Female age	**−2.805**	**0.859**	**−3.267**	0.071	0.184	0.384	**−0.011**	**0.004**	**−2.563**						
Female dispersal status	**1.907**	**0.828**	**2.302**				−0.016	0.015	−1.081						
Distance from nest box to feeder	0.001	0.001	1.014				0.000	0.000	0.454						
Female annual seed consumption	0.001	0.001	0.764	0.000	0.000	0.915				0.000	0.000	−0.216	0.003	0.004	0.736
Lay date				**−0.037**	**0.011**	**−3.291**				**0.101**	**0.019**	**5.196**	**1.036**	**0.253**	**4.090**
Male age										0.466	0.297	1.570	−1.501	3.547	−0.423
Male annual seed consumption										0.001	0.000	1.834	−0.001	0.005	−0.153
Oak density				**0.016**	**0.006**	**2.532**	0.000	0.001	0.719	0.014	0.009	1.507	0.050	0.112	0.450
Year	**19.492**	**0.736**	**26.480**	−0.117	0.274	−0.425	0.013	0.013	0.988	**−1.948**	**0.447**	**−4.360**	**−14.052**	**5.693**	**−2.468**

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effects could still explain increased use of feeders by first-year birds. For instance, adult birds may be more efficient at locating natural food sources through experience, or more likely to monopolise natural food resources by excluding or usurping younger subordinates from rich patches (Krebs et al. 1972, Hegner 1985). Alternatively, basal metabolic rate (BMR) decreases with age across taxa due to physiological changes with age or through selection for low BMRs in food-limited environments (Hulbert and Else 2000, Broggi et al. 2007). Bouwhuis et al. (2011) showed that BMR declines with age in this population of great tits, although the effect (ca 4% decline comparing first year and older birds) is smaller than the difference in estimated seed consumption reported here. A reduction in BMR with age may partially explain why adult birds consumed less supplementary seed than first year birds.

Body size could in part explain the difference between species, as blue tits are around 45% smaller by mass than great tits. Similarly, sex differences in levels of seed consumption are consistent with body size-energetic demand theory, as males are on average 7% greater in mass (Bouwhuis et al. 2014) and 5% longer in wing length in both species. Also, female bills are on average shorter and shallower than males (Gosler 1987). This could make it more difficult for females to de-husk each seed to access the kernel, which may reduce average female seed consumption rate. Sex differences could also be explained by dominance, since in both species, males were found to exploit seed to a greater extent than females.

Individuals were markedly consistent in their exploitation of supplementary food across both weekends and years. Between 33–47% of the overall variation could be explained by individual identity, suggesting intrinsic differences between individuals, perhaps through behavioural tendencies such as personality (Aplin et al. 2013, 2014, 2015), could drive a large part of the observed variation in consumption patterns. Individual consistency in supplementary food consumption may also be explained by location within the wood. The distribution of beech mast (and other natural winter food resources), is non-random and likely to be consistent across time. Therefore, if individuals reside in the same areas of the wood across weekends and years, their dependency upon non-natural food resources is, similarly, likely to remain consistent across time.

Many factors may have prevented the development of carry-over effects in the population. Birds were only provisioned with supplementary food for two days per week. Even with limited weekly availability, individuals could still consume a substantial quantity of supplementary food, with mean values of 815 ± 468 and 527 ± 425 seeds per individual per winter in great tits and blue tits respectively. When accessible, great tits and blue tits consumed on average 40 ± 15 and 23 ± 15 seeds d^{-1} respectively, leading to an estimated gross energetic intake from supplementary food of 31.5 kJ d^{-1} (given a mean estimated energy content of 1.05 kJ $seed^{-1}$). In great tits, estimates of daily energetic expenditure (DEE) range from 88.7 to 105.5 kJ $(24 \ h)^{-1}$ while provisioning young (Tinbergen and Dietz 1994, Tinbergen and Verhulst 2000) and from 50 to 150 kJ $(24 \ h)^{-1}$ during egg laying (Stevenson and Bryant 2000, te Marvelde et al. 2012). DEE increases linearly with decreasing temperature, approaching 130 kJ $(24 \ h)^{-1}$ at ambient temperatures close to 0°C (Sanz et al. 2000). Given this range of DEE estimates, the average energetic intake from sunflower seeds could provide up to 60% of an individual's daily energy requirements. We stress these are rough estimates, as DEE is influenced substantially by a wide range of environmental and intrinsic factors (Tinbergen and Verhulst 2000, te Marvelde et al. 2012).

How the estimated levels of seed consumption we calculate compare to environments where supplementary food is available continuously remains to be determined. A study of feeding in two Nearctic congeners; the black-capped chickadee *Poecile atricapillus* and tufted titmouse *Baelophus bicolor*, found that daily visitation rates at bird feeders ranged from 20–50 visits (Bonter et al. 2013). Assuming that each bird consumed one seed per visit, our daily estimates of seed consumption for blue tits and great tits are similar to those of chickadees and titmice. Therefore, our study population may have consumed around 70% less supplementary food than birds provisioned continuously throughout the winter. Further, birds require daily food to supplement their fat reserves as they can drop by as much as 10% each night (Macleod et al. 2005). By only supplying food for two days per week, natural population regulation processes are likely to have been in operation when food was not available (Lack 1954). Blue and great tits do not store food, so the benefits of supplementary food are likely only to be felt during, and shortly after the periods when it is available. In contrast, caching species such as marsh tits *Poecile palustris* and nuthatches *Sitta europea* could benefit substantially from supplementary food even when it is not available continuously. However, these species respond to the same foraging pressures as non-caching species (Farine and Lang 2013). Whilst previous studies have focussed on continuous provisioning, temporally limiting the supply of food could reduce carry-over effects (both positive and negative). Therefore, further research in now needed to investigate both the influence of different feeding regimes, as well as the relative frequency of typical feeding regimes practiced by the general public.

The seasonal availability of supplementary food may also be important in determining its potential to affect breeding. Here, we withdrew the supplementary food at the end of February so that, in line with Robb et al. (2008b), there was a period of at least 5 weeks between the cessation of supplementary feeding and the commencement of breeding. This gap between feeding and breeding enabled us to distinguish true carry-over effects from directly contemporaneous effects of the supplementary food on body condition and reproduction.

Supplementary food provisioning did not act as an ecological trap; birds were unlikely to use these food resources as a cue for breeding as, in contrast to Robb et al. (2008b), we found no evidence that the degree of individual-level exploitation of supplementary food led to earlier egg laying or increased fledging success. Another potential explanation as to why our findings contrast to those of previous studies is that birds in our study were provisioned with sunflower seeds as opposed to peanuts (Robb et al. 2008b) or fats (Plummer et al. 2013a, b). The nutritional profiles of supplementary foods vary substantially, not only in their energetic content, but also in the levels of vitamins, minerals and antioxidants. Sunflower seeds are particularly high in vitamin E, a key

antioxidant that Plummer et al. (2013b) found could prevent the negative carry-over effects caused by provisioning wild birds with a high-fat supplementary diet. The availability of sunflower seeds as a supplementary food in many ways mimics a large beech mast crop (seeds of beech tree *Fagus sylvatica*); a natural winter food source with substantial annual variation in availability, which both blue and great tits exploit to a large extent when available (Perrins 1966, Savill et al. 2010). The energetic content of beech mast and sunflower seeds are broadly similar, at 24.1 and 24.5 kJ g^{-1} in beech and sunflowers respectively (USDA 2007, Lebl et al. 2010). The abundance of natural winter food resources is widely understood to affect large scale population dynamics in tits (Perrins 1966, Kallander 1981). As such, providing sunflower seeds as supplementary food effectively results in an artificial increase in the frequency of years with high natural food abundance. Therefore, the type of food provisioned could also determine the potential to cause carry-over effects on individuals.

Conclusion

Using RFID technology, we were able to estimate individual consumption of supplementary food in a large wintering population of wild birds. Individuals were consistent in their use of supplementary food resources and variation was explained by species, age, sex, and individual identity. Our results suggest that the quantity of supplementary food consumed by individuals did not impact upon their subsequent reproductive behaviour. Therefore, we demonstrate that with a carefully-designed feeding regime it is possible to monitor the behaviour of birds at a fine scale without affecting their subsequent life histories.

Any negative effects of supplementary feeding are more likely to result from impacts on population-level demographic processes. We found no evidence for a relationship between seed consumption on recruitment or estimated survival with our study design. This suggests that an alternative mechanism could be causing negative effects from constant supplementary feeding, or feeding at more critical time periods (i.e. during breeding). Reduced breeding quality is likely to arise by increasing over-winter survival, which results in greater density-dependent competition, increased use of marginal territories or acquisition of territories by poor-quality individuals (Both 1998, Farine and Sheldon 2015). This mechanism is supported by the fact that first year birds, which are widely thought to be subordinate to older conspecifics, exploited the supplementary food to a greater extent than adults. In common buzzards *Buteo buteo*, supplementary feeding improved breeding success in suboptimal habitat (Rooney et al. 2015), which is likely to increase breeding density. Such density-dependent competition is known to have effects on breeding traits such as recruitment, clutch size and brood mass (Krebs 1970, 1971, Minot 1981, Both et al. 1999). When measured at the population level, these individuals negatively influence mean trait values, such as nestling mass, which can be interpreted as a negative outcome of supplementary feeding. However, this does not necessarily result in a decrease in the population in subsequent years, but rather is the result of natural population regulation processes.

Future experimental studies could attempt to manipulate both the availability and quality of supplementary food to a range of species. These should strive to measure not just the outcome of breeding attempts, but also demographic parameters of the population. The development of new technologies, such as RFID, offer exciting opportunities for experimental tests to explore the potential for supplementary feeding to cause carry-over effects. Feeders can be designed to selectively provision some birds, while excluding others from accessing the feeder (Firth and Sheldon 2015, Firth et al. 2015). This experimental design would limit potentially confounding effects such as year, time and space. Such studies will be valuable from both an ecological as well as an applied conservation perspective.

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Supplementary material (Appendix JAV-00936 at <www.avianbiology.org/appendix/jav-00936>). Appendix 1.