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Does food supplementation really enhance productivity of breeding birds?

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Abstract Food availability influences multiple stages of the breeding cycle of birds, and supplementary feeding has helped in its understanding. Most supplementation studies have reported advancements of laying, whilst others, albeit less numerous, have also demonstrated fitness benefits such as larger clutches, shorter incubation periods, and greater hatching success. Relatively few studies, however, have investigated the effects of supplementary feeding for protracted periods across multiple stages of the breeding cycle. These effects are important to understand since long-term food supplementation of birds is recommended in urban habitats and is used as a tool to increase reproductive output in endangered species. Here, we compare the breeding phenology and productivity of blue tits *Cyanistes caeruleus* and great tits *Parus major* breeding in food-supplemented and non-supplemented blocks in a broadleaf woodland in central England over three seasons (2006–2008). Supplementation was provided continuously from several weeks pre-laying until hatching, and had multiple significant effects. Most notably, supplementation reduced brood size significantly in both species, by half a chick or more at hatching (after controlling for year and hatching date). Reduced brood sizes in supplemented pairs were driven by significantly smaller clutches in both species and, in blue tits, significantly lower hatching success. These are novel and concerning findings of food supplementation. As expected, supplementary feeding advanced laying and shortened incubation periods significantly in both species. We discuss the striking parallels between our findings and patterns in blue and great tit reproduction in urban habitats, and conclude that supplementary feeding may not always enhance the breeding productivity of birds.

Keywords Clutch size · Lay date · Supplementary feeding · Tit · Urban

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Introduction

In recent years supplementary feeding studies of birds have addressed numerous questions, including topics in the fields of evolutionary biology (e.g. de Neve et al. 2007), behavioral ecology (e.g. Grieco et al. 2002), animal physiology (e.g. Schoech et al. 2007), and applied ecology (e.g. Robb et al. 2008b). In these studies, supplementary feeding has involved the provision of quantities and types of food that would not be available naturally. In many studies, particularly of small passerines (e.g. Källander and Karlsson 1993; Nager et al. 1997; Ramsay and Houston 1997), supplements have been provided for relatively short periods, sometimes to examine the importance of food during distinct reproductive phases (e.g. Nilsson and Smith 1988; Nilsson 1994). Little is known about the effects of continuous supplementation across multiple stages of the breeding cycle, and this is important because protracted supplementation of birds is advocated in urban habitats (i.e. year-round—Toms and Sterry 2008) and is also used to increase reproductive productivity in species of conservation concern (e.g. hihi *Notiomystis cincta*—Castro et al. 2003; Florida scrub-jay *Aphelocoma coerulescens*—Schoech et al. 2008).

Although the design of supplementation studies has varied widely, there have been some consistent results. Principally, food supplementation usually advances reproduction (reviewed by Martin 1987; Meijer and Drent 1999; Robb et al. 2008a). In blue tits *Cyanistes caeruleus* and great tits *Parus major* breeding in temperate seasonal latitudes, breeding early in the spring usually enhances reproductive success (Nilsson 2000). For example, early hatched nestlings tend to grow more rapidly (Perrins and McCleery 1989) and show greater long-term survival than those that fledge later in the same breeding season (Norris 1993).

Incubation period also determines breeding phenology, and may also be influenced by food availability, particularly if food is limited and/or energetic costs are high during incubation (Eikenaar et al. 2003). Shorter incubation periods are likely to be beneficial due to earlier hatching (Perrins 1965) and reduced foraging time in incubating adults (Eikenaar et al. 2003). Food supplementation may shorten incubation (e.g. Nilsson and Smith 1988; Sanz 1996), although some studies have found no significant effect (e.g. Nilsson 1994; Nager et al. 1997).

In addition to breeding phenology, food supplementation may influence breeding productivity. Two fundamental determinants of productivity are clutch size and hatching success, parameters that cumulatively determine brood size at hatching (hereafter "brood size"). Clutch size plays a substantial role in determining reproductive rate (the rate at which progeny are produced during an individual's life—Lack 1954) and may be influenced by food availability during egg production (e.g. nutritional constraint—Williams 1996; Ramsay and Houston 1998) and after laying (e.g. food availability when rearing young, mediated by the rearing capacity of individual pairs—Lack 1954; Pettifor et al. 1988). Despite the importance of food availability, food supplementation studies have produced mixed results (e.g. reviewed by Martin 1987; Boutin 1990), with significant positive associations between clutch size and supplementation found in some (e.g. Soler and Soler 1996; Nilsson 1991) but not others (e.g. Davies and Lundberg 1985; Svensson and Nilsson 1995). Similarly, hatching success has sometimes increased due to supplementation (e.g. Nilsson and Smith 1988), but most studies show no significant effect (e.g. Ewald and Rohwer 1982; Arcese and Smith 1988). As a corollary, supplementation has either increased brood size or had no significant effect.

Here, we report the influence of continuous food supplementation from several weeks pre-laying through to hatching on the breeding phenology and productivity of blue and great tits in three successive years. Blue and great tits are ideal focal species because they are quick to explore novel objects (e.g. feeders) and take readily to nestboxes (Perrins 1979), enabling breeding parameters to be recorded easily. We hypothesized that food supplementation would: (1) advance clutch initiation; (2) enlarge clutch size; (3) shorten incubation period; (4) enhance hatching success; and (5) enlarge brood size.

Materials and methods

Study site and experimental design

The study was conducted over three breeding seasons (2006–2008) at Chaddesley Woods National Nature Reserve, a 101-hectare woodland in Worcestershire, UK (UK Ordnance Survey Grid Reference: SO914736, 52.36 N, −2.14 E). The study area consisted of three treatment blocks, each containing 96 nestboxes arranged on a square grid at ca. 40 m spacing (ca. 6.25 nestboxes ha^{-1}). This nestbox density is comparable to other established nestbox studies of tits in similar habitats (e.g. Minot and Perrins 1986; Mänd et al. 2005). In food-supplemented blocks there were 24 feeders, with one feeder placed centrally in the quincunx formed by each set of four nestboxes and a feeder, so that each nestbox was ca. 28 m from a feeder. The habitat in each treatment block was similar, consisting of broadleaf, deciduous woodland, predominantly oak *Quercus* spp. There was a buffer strip of ca. 90 m width between nestboxes on the perimeter of one treatment block and the closest feeders in an adjacent block. Although it is possible that some "crossing-over" between treatments may have occurred (see Wilkin et al. 2009 for details of parid foraging ranges), blue and great tits are territorial from January, becoming increasingly so as spring approaches (Gosler 1993). Therefore, access to peanut cake is likely to have been markedly lower in control (compared with supplemented) birds. Nestboxes were tree-mounted ca. 2 m above the ground, and the 32 mm entrance holes faced NE (away from the prevailing SW winds).

Food supplementation

In each year of the study, one treatment block received no supplementary food (hereafter "control"), and two treatment blocks received peanut cake (comprising 50% ground peanuts and 50% beef tallow; hereafter "supplemented"). Peanut cake is an energy-rich commercial bird food (CJ Wildlife Ltd., Upton Magna, UK). Both species were observed feeding on this supplement throughout the study. Peanut cake was provided from early March (ca. 4–5 weeks pre-laying) to the end of July (ca. 6–8 weeks post-fledging) each year. Hatching usually occurred in early- to mid-May, at which point an additional food supplement was added in one of the two supplemented treatment blocks. This paper summarizes the effects of supplementation prior to the addition of this third treatment. Feeders were checked regularly (ca. twice a week—each peanut cake weighed 500 g and usually lasted over a week) and were replenished upon marked depletion so that peanut cake was provided ad libitum. Occasional heavy utilization (e.g. by grey squirrels *Sciurus carolinensis*) disrupted this supply, but such interruptions were brief (ca. 1–2 days). Dietary treatments were rotated over the three study years, so that each treatment block was supplemented twice and was the control once.

Breeding parameters

Clutch initiation dates were determined by visiting nestboxes twice a week and noting the day on which the first egg was laid or by back-counting eggs (assuming one egg was laid per day—Perrins 1979) when two or more eggs were already present. Visits to nestboxes were made after 0800 hours, since blue and great tits usually lay at around 0600 hours (Perrins 1979). Clutch size and clutch completion date were recorded by monitoring nestboxes in which eggs had been laid every 1–2 days until no more eggs were laid. Incubation period was defined as the number of days between clutch completion date (day 0) and hatching date of the first egg (Cresswell and McCleery 2003). A mean incubation period of ca. 12–13 days was expected (Perrins 1979; Cresswell and McCleery 2003); therefore, hatching checks were carried out on a daily basis from 10 days after clutch completion until the first egg hatched. Blue and great tits do not remove unhatched eggs from their nests (Kempenaers et al. 1998; TJEH, pers. obs.), so unhatched eggs were counted ca. 20 days after hatching (when fledge checks were conducted). Hatching success was defined as the number of eggs in a clutch that hatched as a proportion of the clutch size. Brood size was calculated as the clutch size minus any unhatched eggs (i.e. the maximum possible brood size), to eliminate the influence of early nestling-phase mortality.

Statistical analysis

All statistical analyses were carried out using PROC GLIMMIX in SAS (SAS Institute Inc. 2008) or Minitab 15 (Minitab 2007). Combined-year analyses were conducted unless the influence of supplementation differed significantly between years (year × dietary treatment: $P \leq 0.05$), in which case within-year analyses were conducted. Nestbox nested in treatment block was specified as a random factor in combined-year analyses due to repeated measures on nestboxes and blocks, and spatial nesting of nestboxes within blocks. In within-year analyses, treatment block was specified as a random factor. Analyses of clutch initiation date and incubation period were fitted with normal errors after examining model fit (generalized chi-square/DF = ca. 1). Poisson errors were fitted in clutch and brood size analyses, whereas binomial errors were specified in hatching success analyses (binomial logistic regression, with number of eggs hatched as a proportion of the clutch size as the response variable).

Only first clutches were considered in all analyses. Clutch initiation date analyses included all first clutches, while analyses of clutch size excluded clutches that were abandoned prior to clutch completion and specified clutch initiation date as a covariate (due to seasonal decline in clutch size—Perrins and McCleery 1989). Incubation period analyses only included clutches that hatched, and clutch completion date and clutch size (which may both influence incubation period—Perrins 1979; Gosler 1993; Deeming 2002) were included as covariates. Hatching success and brood size analyses only included nests in which hatching occurred, and hatching date was specified as a covariate (due to seasonal decline in hatching success and brood size—Perrins 1979). Clutches with laying breaks >2 days were excluded from clutch size, hatching success, and brood size analyses. Two clutches that were apparently abandoned prior to the eventual onset of incubation were excluded from incubation period, hatching success, and brood size analyses.

Colinearity between covariates within each model (where applicable) was low (Spearman's rank correlation: all r^2 values ≤ 0.02). Covariate × dietary treatment interactions were tested to examine whether covariate effects were consistent between treatments. We had no a priori expectation that these interactions would be significant, so these terms were not included in all models; instead, they were tested for significance independently of one another. If more than one interaction was significant, all were included in the final model provided that each remained significant. Nonsignificant interactions ($P > 0.05$) were removed if there was no significant change in model deviance where applicable. Details of the final model for each breeding parameter, including statistics for each predictor, are provided in S1 of the "Electronic Supplementary Material" (ESM).

Data from combined years are presented in the figures except where there was a significant year × treatment interaction ($P \leq 0.05$), in which case data from individual years are shown. All figures were plotted as means ± 1 standard error from statistical estimates (illustrating the effects of treatment after controlling for other predictors in the final model—see S1 of the ESM). For models with non-normal errors, standard errors were calculated using the delta method (Oehlert 1992). In the "Results", the magnitudes of the effects of supplementation are described by comparing the means presented in the figures.

Results

Food supplementation advanced clutch initiation date significantly in both species (mean advancement in blue tits: 2.0 days; $F_{1,187} = 11.06$, $P = 0.001$; great tits: 3.0 days; $F_{1,86} = 22.51$, $P < 0.001$; Fig. 1a). Clutch size in both species was reduced significantly as a result of supplementation (mean reduction in blue tits: 0.4 eggs; $F_{1,151} = 7.65$, $P = 0.006$; great tits: 0.7 eggs; $F_{1,81} = 10.10$, $P = 0.002$; Fig. 1b).

The effect of supplementation on incubation period duration varied significantly between years (year × dietary treatment in blue tits: $F_{2,149} = 8.44$, $P < 0.001$; great tits: $F_{2,70} = 6.66$, $P = 0.002$). Supplementation shortened incubation periods in blue tits significantly in 2006 (mean reduction: 0.6 days; $F_{1,125} = 9.44$, $P = 0.003$) and 2008 (mean reduction: 1.2 days; $F_{1,98} = 17.98$, $P < 0.001$), but had no significant effect in 2007 ($F_{1,139} = 0.32$, $P = 0.57$; Fig. 2a). However, in great tits, incubation periods were shortened significantly by supplementation in each year (mean reduction in 2006: 1.2 days; $F_{1,60} = 30.05$, $P < 0.001$; 2007: 0.5 days; $F_{1,71} = 6.88$, $P = 0.01$; 2008: 0.4 days; $F_{1,100} = 4.32$, $P = 0.04$; Fig. 2b). The influence of clutch completion date and clutch size on incubation period showed some differences between treatments (see interactions in S1 of the ESM), but these differences were not consistent between years or species.

Hatching success was significantly lower in supplemented compared with control blue tits (mean reduction: 1.4%; $F_{1,132} = 8.10$, $P = 0.005$; Fig. 3a), but great tits showed no significant differences between treatments ($F_{1,71} = 0.22$, $P = 0.64$; Fig. 3a). Hatching success in supplemented blue tits increased throughout the breeding season, but the opposite was found in control conspecifics (hatching date × dietary treatment: $F_{1,132} = 6.65$, $P = 0.01$).

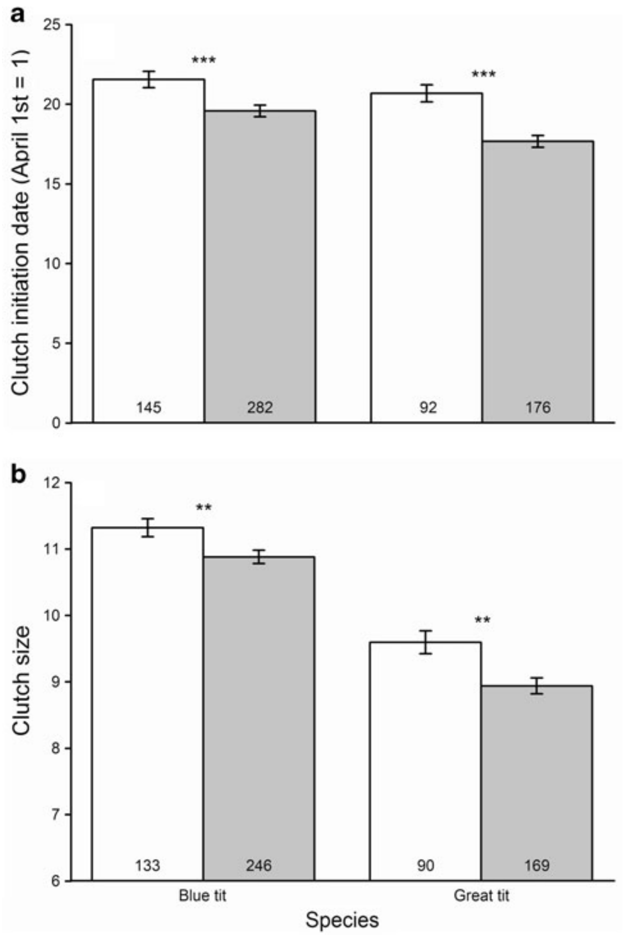

Fig. 1 **a** Clutch initiation date and **b** clutch size (both mean ± 1 standard error) of first clutches of non-supplemented control (*open bars*) and peanut cake supplemented (*filled bars*) blue and great tits at Chaddesley Woods National Nature Reserve in 2006–2008. ***$P \leq 0.001$, **$P \leq 0.01$. Sample sizes are shown inside *bars*. See S1 of the "Electronic Supplementary Material" for statistical findings, and see text for details

Brood size in both species declined significantly as a result of supplementation (mean reduction in blue tits: 0.6 chicks; $F_{1,129} = 8.28$, $P = 0.005$; great tits: 0.5 chicks; $F_{1,69} = 5.51$, $P = 0.02$; Fig. 3b). In great tits, brood size increased with later hatching in supplemented pairs, but the opposite was found in controls (hatching date × dietary treatment: $F_{1,69} = 4.42$, $P = 0.04$).

Discussion

Continuous food supplementation throughout multiple stages of the breeding cycle had pronounced effects on breeding phenology and productivity of blue and great tits. As hypothesized, food supplementation advanced clutch initiation (Fig. 1a) and shortened incubation periods (except in blue tits in 2007) significantly in both species (Fig. 2).

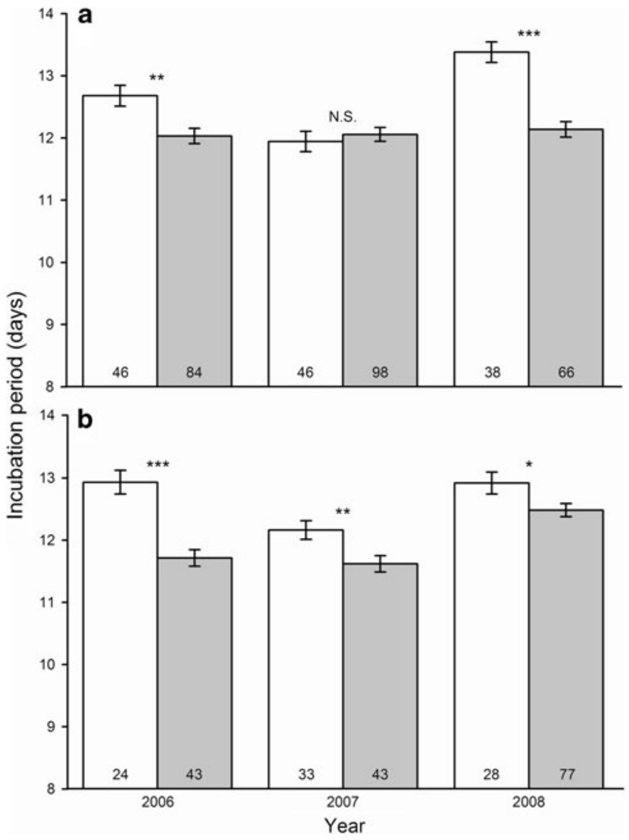

Fig. 2 Incubation period length (mean ± 1 standard error) of first clutches of non-supplemented control (*open bars*) and peanut cake supplemented (*filled bars*) **a** blue and **b** great tits at Chaddesley Woods National Nature Reserve in 2006–2008. ***$P \leq 0.001$, **$P \leq 0.01$, *$P \leq 0.05$, *N.S.* not significant. Sample sizes are shown inside *bars*. See S1 of the "Electronic Supplementary Material" for statistical findings, and see text for details

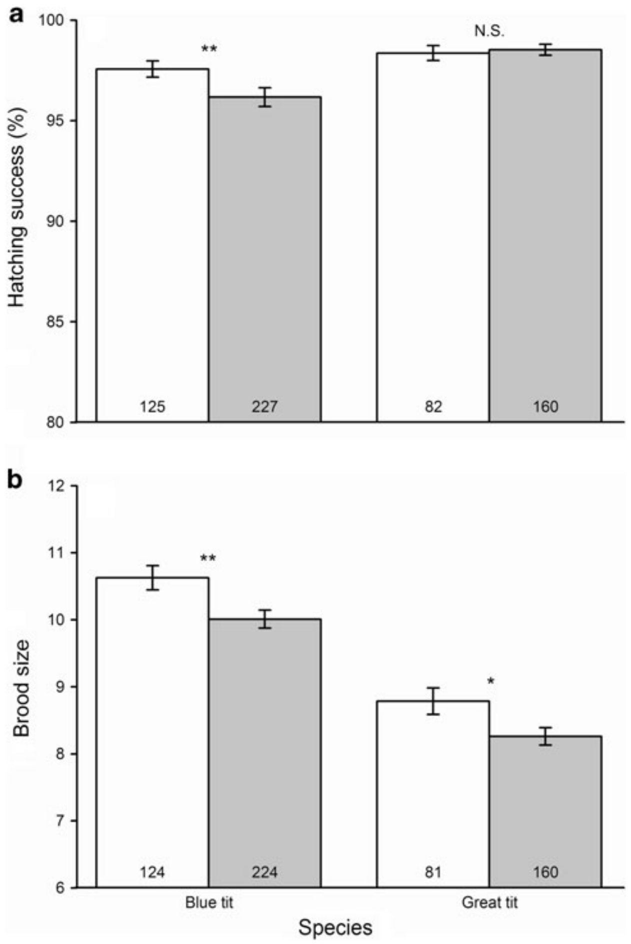

Fig. 3 **a** Hatching success and **b** brood size (both mean ± 1 standard error) of first clutches of non-supplemented control (*open bars*) and peanut cake supplemented (*filled bars*) blue and great tits at Chaddesley Woods National Nature Reserve in 2006–2008. **$P \leq 0.01$, *$P \leq 0.05$, *N.S.* not significant. Sample sizes are shown inside *bars*. See S1 of the "Electronic Supplementary Material" for statistical findings, and see text for details

Advanced laying is consistent with most previous supplementation studies, although shorter incubation periods have been reported less widely (S2 of the ESM). Contrary to our hypotheses, clutch (Fig. 1b) and brood (Fig. 3b) sizes in both species were reduced significantly by supplementation. Furthermore, hatching success was significantly lower in supplemented blue, but not great, tits (Fig. 3a). To our knowledge, reduced clutch size as a result of supplementation is a novel finding in passerines (reported in one previous study of birds: American coots *Fulica americana*—Hill 1988) (S2 of the ESM). Reduced hatching success and brood size are, to our knowledge, unique findings (S2 of the ESM). Below, we consider the fitness consequences and possible mechanisms underlying these results. We also discuss the applied importance of our findings.

Clutch initiation date

In seasonal environments, initiating clutches early in the breeding season may bring fitness gains to parents and young. Among blue and great tits, early-laid clutches hatch nestlings that tend to grow rapidly due to the close synchronization of nestling peak food demand with a peak in the abundance of caterpillars, the most common food provisioned to nestlings (Cramp and Perrins 1993a, b). Furthermore, the probability of recruitment into the breeding population declines with later fledging (Verhulst and Tinbergen 1991). However, there are fitness costs associated with breeding too early, including reduced survival of juveniles and breeding females (Norris 1993; Nilsson 1994). The optimality of different laying dates in our study population, therefore, merits further investigation.

The mechanisms by which food supplementation promotes early laying are difficult to elucidate. Early laying may be constrained in seasonal environments due to the substantial nutritional requirements of egg formation (the constraint hypothesis: Perrins 1965; Lack 1966). Were this to apply to our study, supplementation may have advanced laying by facilitating the earlier attainment of nutritional thresholds and/or the sequestration of other, potentially limiting, nutrients (e.g. calcium: Reynolds et al. 2004; protein: Schoech et al. 2004). Alternatively, rather than influencing a nutritional constraint, it is possible that increased food availability early in the breeding season acts as a cue that richer foraging conditions at a key point later in the breeding cycle, for example during chick rearing, are relatively advanced (the cue/anticipation hypothesis: Lack 1954; Perrins 1965). Supplementation may have acted directly or indirectly as a predictive cue: directly if perceived as a resource that was suitable to feed young; indirectly if peanut cake enabled more time and/or greater success in foraging for natural food items that, in turn, acted as a cue to clutch initiation. Indeed, supplementation may have acted directly or indirectly throughout the breeding cycle. A third possibility is that supplementation advanced settlement onto breeding territories (Kelly and Van Horne 1997), perhaps because birds that settled in the control treatment competed initially for a supplemented territory.

Some predictors of clutch initiation date are difficult to investigate in this study because not all breeding adults were caught. For example, there may be carryover effects of dietary treatment from the previous year (Grieco et al. 2002). However, advanced laying due to supplementation was recorded in all three years in both species, including the first year of the study in the absence of such carryover effects. Laying tends to be earlier in resident and older tits (Nager and van Noordwijk 1995), and the ratio of resident to immigrant birds and/or the age structure of the breeding population may have differed between treatments. The latter seems unlikely, however, since older females usually lay larger clutches (Perrins 1979), but this was not found in the supplemented treatment (Fig. 1b).

Clutch size

The optimization of clutch size has been studied widely (individual optimization hypothesis: Lack 1954, 1966; Charnov and Krebs 1974; Perrins and Moss 1975; Gustafsson and Sutherland 1988; Pettifor et al. 1988). For short-lived species such as blue and great tits, clutch size is likely to be optimized within each breeding season to maximize the number of young recruited into the breeding population—mediated on an individual basis by the rearing capacity of each pair. Evidence has been found in support of such optimization (e.g. Pettifor et al. 1988), but other studies have found a mismatch, usually biased towards clutch sizes that are sub-optimally small (reviewed by Lessells 1986; but see Rytkönen and Orell 2001). If future conditions are unpredictable at the point of laying, conservative clutch sizes may, in evolutionary terms, be most productive (Charnov and Krebs 1974; Perrins and Moss 1975). In our study, supplementation, presumably, reduced any nutritional constraints on egg production and "insulated" blue and great tits against unpredictable future conditions (e.g. reduced food availability—Schoech et al. 2008). In these respects, and since larger clutches usually produce a greater number of recruits into the breeding population (Boyce and Perrins 1987), the reduction of clutch size due to supplementation is difficult to interpret.

The availability of protein—or perhaps, more specifically, essential amino acids (Ramsay and Houston 1998)—may limit egg production (Jones and Ward 1976; Williams 1996; but see Nager et al. 1997), and peanut cake may have influenced smaller clutch sizes because it is fat-rich and protein-poor (e.g. compared with other common bird-food supplements, % fat and protein respectively: peanut cake 70.5 and 17.1; peanuts 44.5 and 28.7; black sunflower seeds 44.4 and 18.0; sunflower hearts 58.0 and 21.4—Chris Whittles, pers. commun.). Significant consumption of peanut cake might have reduced clutch size through insufficient sequestration of protein (or other limiting nutrients). Low protein intake at the point of laying may also act as a predictive cue to low protein availability later in the season (Drent and Daan 1980). A substantial amount of protein-rich food is required to rear chicks successfully (Gosler 1993), and this could drive clutch size.

Smaller clutches enable earlier hatching within the season, and this often has fitness benefits (see above). Therefore, supplemented birds may have reduced clutch size to facilitate earlier hatching. However, in Wytham Woods (Oxfordshire, UK), the fitness gains of earlier hatching (more young recruited into the breeding population) fail to explain satisfactorily the small clutch sizes of great tits, since larger clutches almost always produce more recruits (Perrins and McCleery 1989). If blue and great tits in our study population also lay clutch sizes that are conservative, it is likely that a further reduction (i.e. due to supplementation) will reduce the number of recruits per brood.

Rather than being a poor quality supplement, peanut cake might be of high quality with respect to adult maintenance (albeit not reproduction) and enhance adult survival (e.g. Jansson et al. 1981). Smaller clutches (Fig. 1b) represent a smaller investment in current reproduction (in absolute terms), and this may increase adult survival. However, there is little evidence for this (e.g. Pettifor et al. 1988), although such findings have not been made in the context of supplementary feeding. Despite this, both species are relatively short-lived and future reproduction may be of secondary importance in shaping life-history traits compared with current reproduction (Blondel et al. 1998). Within years, second broods were not found in blue tits and were exceptionally rare in great tits. Therefore, in both species, reduced investment in the size of first clutches in supplemented birds was not compensated for by more breeding attempts in each year.

Finally, increased breeding density is known to reduce clutch size in both species (e.g. Perrins 1965; Perrins and McCleery 1989; Wilkin et al. 2006), and this might explain our treatment effects. However, in blue tits, nestbox occupancy (recorded when laying occurred), which may be a surrogate for minimum breeding density (we do not have data for natural cavities), did not differ significantly between treatments (combined years: $F_{1,573} = 0.17$, $P = 0.68$). In great tits, the influence of supplementation on occupancy differed significantly between years (treatment × year: $F_{2,571} = 3.41$, $P = 0.03$), but was only significant in 2007 when occupancy in control territories was significantly higher (control = 38.5%, supplemented = 24.0%; $F_{1,286} = 6.48$, $P = 0.01$). Total occupancy (blue and great tits combined) tended to be greater in the control treatment (control = 87.9%, supplemented = 84.2%; $F_{1,573} = 3.41$, $P = 0.07$). Therefore, the smaller clutch size of supplemented birds is even more remarkable. Moreover, clutch size declined with later laying in both species, so advanced laying in supplemented birds (Fig. 1a) should have promoted larger, rather than smaller, clutches.

Incubation period

Shorter incubation periods are likely to be adaptive. For example, there are fitness benefits associated with earlier hatching, and eggs and nestlings are more vulnerable to predation than fledged young (i.e. truncation of these formative stages is likely to be beneficial—Bosque and Bosque 1995).

Food supplementation may have shortened incubation periods through greater incubation attendance (Eikenaar et al. 2003), perhaps driven by increased foraging efficiency of females and/or increased courtship feeding of the female by her mate (Nilsson and Smith 1988). Furthermore, supplemented females may have commenced incubation with enhanced body condition compared with controls and, as a result, foraged less during incubation (Wiebe and Martin 2000). However, rather than influencing incubation efficiency, supplementation may advance incubation onset relative to the laying sequence, perhaps to maintain perceived synchrony with natural food resources (e.g. caterpillars—Cresswell and McCleery 2003). Nilsson (1994) found that blue tits that were supplemented throughout egg-laying until incubation initiated incubation earlier relative to clutch completion date compared with conspecifics that had supplements removed at the onset of laying or non-supplemented controls. Although advanced hatching may have fitness benefits, achieving this via advanced onset of incubation relative to the laying sequence may cause greater hatching asynchrony (Cresswell and McCleery 2003; Eikenaar et al. 2003) and subsequent brood reduction and/or lower hatching success (Perrins 1979; Nilsson 1993). The influence of supplementation on incubation period was not consistent in all years (Fig. 2), and this is difficult to explain. Furthermore, the influence of clutch completion date and clutch size on incubation period showed some differences between treatments, but these effects were not consistent (see interactions in S1 of the ESM).

Hatching success

Hatching success determines the efficiency by which investment in egg production is carried forward into the chick-rearing phase. Reduced hatching success is likely to be deleterious since egg production is expensive energetically, nutritionally, or both (Robbins 1981; Walsberg 1983), and more investment (e.g. heat—Wiebe and Martin 2000) may be required to incubate larger clutches.

Hatching success is likely to be influenced by incubation behavior (Perrins 1979; Lyon and Montgomerie 1985), and egg size and nutritional content (Amundsen et al. 1996; Saino et al. 2004). If shorter incubation periods in supplemented compared with control blue tits (2006 and 2008) (Fig. 2a) and great tits (2006–2008) (Fig. 2b) were caused by greater incubation attendance (e.g. Eikenaar et al. 2003), enhanced, not reduced, hatching success would be expected (Lyon and Montgomerie 1985; Nilsson and Smith 1988). If, however, shorter incubation periods resulted from supplemented females initiating incubation earlier in the laying sequence, we might have expected hatching asynchrony (Cresswell and McCleery 2003) and reduced hatching success as a result (Perrins 1979). However, reduction of hatching success in supplemented (compared with control) blue tits was greatest in 2007 when incubation period did not differ significantly between treatments (Fig. 2a). Furthermore, hatching success in great tits showed the least difference in 2006 when incubation periods were shortened most significantly by supplementation (Fig. 2b).

Larger eggs typically contain greater absolute quantities of nutrients (Ankney and Johnson 1985; Rohwer 1986), and may have greater hatching success (Perrins 1979; Amundsen et al. 1996; Saino et al. 2004). However, in absolute terms, differences in egg mass between treatments were small, and egg composition (water content, and the dry mass of shell, yolk, and albumen) also showed few differences (Harrison 2010). Interestingly, hatching success in supplemented blue tits increased throughout the breeding season, but the opposite was found in control nests (hatching date × dietary treatment—S1 of the ESM). This indicates further subtle effects of supplementation that are, currently, difficult to interpret.

Brood size

Unless broods are very large (e.g. > ca. 10 in great tits), increased brood size normally results in a greater number of surviving young (Perrins and Moss 1975). Since mean brood sizes were not especially large in our study population (Fig. 3b), it is probable that larger broods were more productive. However, the survival probability of individual fledglings decreases with increased brood size (Gustafsson and Sutherland 1988; Naef-Daenzer et al. 2001), often as a result of decreased nestling growth (Perrins 1965; Nur 1984) and/or later hatching (Perrins and McCleery 1989). It is possible, therefore, that smaller broods in supplemented birds represented a fine-tuning of reproductive investment.

Smaller brood sizes in supplemented pairs were driven by significantly smaller clutch sizes (Fig. 1b), and, in blue tits, significantly lower hatching success (Fig. 3a). Clutch size may have been reduced strategically in supplemented birds, but an adaptive reduction of hatching success in blue tits seems implausible due to the nutritional costs and time delay caused by unnecessary egg production. As expected, brood size decreased throughout the breeding season in blue tits and non-supplemented great tits. However, brood size in supplemented great tits increased throughout the breeding season (S1 of the ESM), perhaps because of a relative “underperformance” of early-breeding pairs and/or because later-breeding pairs were “insulated” from declining peaks of natural foods. Supplementation can, therefore, disrupt normal patterns of reproduction in this species.

Applied importance

Many of our results of food supplementation were unexpected (i.e. smaller clutch and brood sizes in both species, and lower hatching success in blue tits). However, there are striking similarities with the reproduction of blue and great tits in urban habitats, in which food supplementation is common (Jones and Reynolds 2008; Robb et al. 2008a). In urban habitats, both species initiate clutches earlier than in nonurban ones and lay smaller clutches (reviewed by Chamberlain et al. 2009). Furthermore, in a study of blue and great tits across the UK, Harrison (2010) found that increased urbanization correlated significantly with smaller broods in both species and with reduced brood size as a proportion of clutch size (perhaps caused by lower hatching success) in blue, but not great, tits.

The applicability of our findings to urban areas should, however, be treated with caution due to marked habitat differences. Furthermore, other factors in addition to supplementary feeding may influence reproductive parameters of birds in urban habitats (e.g. temperature—Visser et al. 2009; pollution—Eeva et al. 1997; lower natural food availability—Perrins 1965). However, we supplemented peanut cake (a common garden bird-food), throughout the breeding season (as recommended in gardens—Toms and Sterry 2008), to blue and great tits (species that commonly breed in UK gardens—Bland et al. 2004). Although logistically challenging, further research in urban/garden habitats would clearly be of value (Jones and Reynolds 2008) to explore the broader applicability of our findings.

Food supplementation is also employed to increase reproductive productivity in species of conservation concern (e.g. Castro et al. 2003; Houston et al. 2007; Schoech et al. 2008). Such supplementation is often practiced in the “natural” breeding habitats of these species, and, to this end, our findings are highly applicable. The concerning findings of our study suggest that new supplementation initiatives should only be implemented after smaller-scale feeding trials, especially if dealing with discrete populations, since the effects of supplementation can vary geographically (e.g. Schoech and Hahn 2008) and intraspecifically (e.g. Nager et al. 1997; Ramsay and Houston 1997; this study). Indeed, whilst food supplementation may have pronounced fitness benefits (e.g. Schoech et al. 2008), our study demonstrates that it may not be a panacea.

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