



In Focus

Featured Articles in This Month's *Animal Behaviour**Extra Rations Delay the Dawn Chorus*

Almost half the households in the U.K. provide food for garden birds, and it has been calculated that the amount of wild bird food sold per year could, hypothetically, feed 30 million great tits. The same is true for the U.S. We are, it seems, engaged in a giant ecological experiment. It has been known that such food supplements can advance egg-laying dates and also increase fledging success, but what about other effects on behaviour? In this month's issue (pp. 361–365), Katja Saggese, Fränzi Korner-Nievergelt, Tore Slagsvold and Valentin Amrhein investigate how male singing behaviour, specifically the tendency of male great tits to sing before dawn during the breeding season, is influenced by supplementary feeding.

Male great tits establish breeding territories in the spring, and sing before dawn—the famous dawn chorus—during this period. Given that singing is energetically expensive and that it has to be traded off against other activities, such as foraging, providing males with food can be expected to influence their singing behaviour. Extra food could, for example, attract other males to the territory, so that the territory owner has to invest more energy in defence, whether by singing or actively chasing intruders away. In addition, theoretical models suggest that extra food should lead males to sing earlier in the morning or increase the effort they put into their singing bouts. Studies supporting these predictions have been conducted before, but the period of supplementary feeding has been very short, around 1–5 days, so Saggese and colleagues decided to investigate what would happen if supplementary feeding was extended. They provided supplementary food to males for a period of 2 weeks, so that males received extra food until about 3 weeks before the start of the egg-laying period.

Males in territories with extra food were found to start singing later relative to sunrise than males in unsupplemented territories (Fig. 1). In 36% of observation sessions, supplemented males started to sing only after the sun had risen, skipping their regular dawn singing session. Extra food did not, however, affect the male's song output. The late morning start of supplemented males also continued for 2 weeks after the end of supplementary feeding.

Given that theoretical considerations suggest supplemented males should start singing earlier, these results are both surprising and intriguing. One suggestion is that males postpone singing because they can eat human-provided food in the dark, which isn't possible for their natural insect-hunting behaviour. As the researchers never saw a single great tit male feeding before sunrise, however, this explanation seems unlikely.

Another possibility is that the extra food attracted other great tit males to the scene, and so required males to invest in extra defence but, again, Saggese and colleagues found no evidence of more great tit intruders in supplemented territories. A third possibility is that



Figure 1. Supplementary food in their territories leads male great tits to delay their morning singing bouts. Photo: Soenke Morsch.

more predators would be attracted to territories with a reliable supply of food in a particular location, and so males may have avoided singing before dawn to reduce their predation risk. The likelihood of this as an explanation must be tempered, however, by the fact that males continued to delay singing for 2 weeks after feeding was discontinued; as Saggese and colleagues note, it would be surprising if predation risk continued to be elevated for this long.

So why would males continue singing later once the extra food was removed? Saggese et al. suggest that supplemented males could have acquired higher energy reserves or their perception of territory quality could have changed. It is also possible, however, that males could have continued to get food from other human-provided sources, or that the quality of the supplementary food could have changed the nature of their territorial behaviour.

At present, we don't have any good answers to these questions, nor is it apparent why this longer-term study should show different results to short-term supplementation. Clearly, replication of this study is needed to determine whether the effect is robust, and to tease out why longer-term supplementation should have these effects. Indeed, Saggese and colleagues actively encourage further experiments so that we can get a more precise handle on how and why supplementary feeding changes male territorial behaviour in these long-lasting ways, as well as understand how such feeding might also influence female behaviour.

Louise Barrett
Executive Editor



Articles

Wild bird feeding delays start of dawn singing in the great tit

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Supplementary feeding of wild birds during winter is one of the most popular wildlife management activities, and is likely to have profound influence on the behavioural ecology of a species. At garden bird feeders, birds are now often fed well into the breeding season. Providing food within an established songbird territory, however, is likely to influence the territorial behaviour of the resident male. We used song performance during the dawn chorus in early spring to study behavioural changes in food-supplemented great tits, *Parus major*. After 2 weeks of continuous food supply within their territory, supplemented males started dawn singing later than control males, and thus postponed their regular dawn chorus before sunrise. This effect was maintained 2 weeks after food supplementation had ended. However, we did not find an effect of long-term feeding on song output. Our results were largely unexpected because formal models and field studies on short-term food supplementation suggested an earlier start of dawn singing or a higher dawn song output. Because we did not observe great tits visiting the feeders before sunrise or food supplementation increasing the numbers of conspecific intruders, the reasons for the delay in the start of dawn singing remain unclear; possible explanations include the presence of predators at feeding stations and the quality of the supplementary food itself. Delaying dawn singing could potentially affect the reproductive success of supplemented males, for example if females base extrapair mating decisions on dawn song performance of their mates.

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In many countries, providing food for wild birds is common practice. In the U.K., about 48% of households provide supplementary food for birds (Davies et al. 2009), and sufficient commercial wild bird foods are sold to support a hypothetical number of over 30 million great tits, *Parus major* (Robb et al. 2008a). In the United States, an estimated 60 million people, or 43% of households, are reported to feed wild birds (Martinson & Flaspohler 2003). While this enormous feeding effort is likely to have profound influence on the ecology of a species, surprisingly little is known about the impact on behaviour of individual birds (Jones & Reynolds 2008; Robb et al. 2008b). Supplementary feeding that is restricted to the winter period has been shown to carry over

to the subsequent breeding season by advancing laying dates and increasing fledging success, for example in the blue tit, *Cyanistes caeruleus* (Robb et al. 2008a, b). However, although feeding of wild birds was originally aimed to help them survive the winter, city birds are now often fed well into the breeding season or even year-round (Jones & Reynolds 2008).

Providing food in early spring within an established territory of a garden bird is likely to influence the territorial behaviour of the resident male. For example, supplementary food may attract conspecific males (Davies & Houston 1981; Tobias 1997; Berg et al. 2005), which can force the resident to defend its territory more vigorously by attacking the intruders (Ydenberg 1984; Tamm 1985; Tobias 1997) or by increasing song output (Cuthill & Macdonald 1990). Furthermore, song output of a male songbird is likely to be constrained by its energy reserves, and singing also conflicts temporally with foraging (Gil & Gahr 2002; Berg et al. 2005). Accordingly, as reviewed by Thomas (1999), a number of studies have found that food-supplemented males increased song output during the day. This effect was predicted by formal models on daily singing and foraging routines in birds (McNamara et al. 1987; Hutchinson et al. 1993; Hutchinson 2002). The models were mainly concerned

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with explaining a peak of singing that in many species occurs during the dawn chorus in the hour before sunrise (Staicer et al. 1996).

We studied effects of supplementary feeding on dawn singing in early spring, in one of the best-known visitors at Eurasian garden feeders, the great tit. From at least 6 weeks before egg laying until after the incubation period of females, great tit males usually sing at much higher levels shortly before sunrise than after sunrise or at other times of the day (Amrhein et al. 2008). As in other bird species, singing during the dawn chorus may serve mate attraction, mate guarding or territorial defence (Mace 1987; Slagsvold et al. 1994). In two related species, an early starting time of singing and a high song output during the dawn chorus reliably indicate the quality of a male (black-capped chickadee, *Parus atricapillus*: Otter et al. 1997; blue tit: Poesel et al. 2006). In the great tit, dawn song output or start of dawn singing can indicate anthropogenic chemical pollution (Gorissen et al. 2005) and light pollution (Kempnaers et al. 2010). Moreover, studies on the winter wren, *Troglodytes troglodytes*, found that the starting time of singing and number of songs sung before sunrise particularly sensitively reflect territorial intrusions by conspecific males (Amrhein & Erne 2006; Erne & Amrhein 2008; Amrhein & Lerch 2010), which in the present study could be attracted by supplementary food. We therefore chose the starting time of singing and dawn song output as response variables to study the effects of wild bird feeding on territorial behaviour of male great tits.

Short-term supplementary food provisioning for 1–5 days is known to lead to an earlier start of dawn singing or to a higher dawn song output in the blackbird, *Turdus merula* (Cuthill & Macdonald 1990), the silveryeye, *Zosterops lateralis* (Barnett & Briskie 2007) and the black-capped chickadee (Grava et al. 2009). However, to investigate realistic effects of wild bird feeding, food needs to be regularly provided for longer periods of time, and also possible long-term effects on behaviour beyond the end of food provisioning should be taken into account (Jones & Reynolds 2008; Robb et al. 2008a). As suggested by several authors (Cuthill & Macdonald 1990; Thomas 1999; Berg et al. 2005), long-term manipulation of food availability may affect variables such as the frequency of territorial intrusions that will in turn influence song output in complex ways. In this study, we aimed to investigate whether regular wild bird feeding in early spring has enhancing effects on song performance of territorial songbirds, as suggested by previous studies on short-term food supply. Alternatively, long-term feeding might lead to unpredicted changes in singing behaviour, and such changes could also last beyond the end of food provisioning.

METHODS

The study was conducted in a 1.6 km² nestbox plot adjacent to the suburbs of Oslo, Norway, from 7 March to 30 April 2007. Our subjects were 28 colour-banded males (14 supplemented males and 14 controls). Of the 19 birds of known age, seven were 1 year old ('yearlings', four supplemented birds, three controls) and 12 were older (five supplemented birds, seven controls). All subjects were separated by at least two territories from each other and potentially had access to private garden feeders up to 500 m from their territories.

Subjects were observed at dawn on three mornings, with 16–17 days between observation sessions. The first observation session served as a control without supply of supplementary food. Immediately after the first observation session, a feeder was provided within the territory. Supplemented males drawn at random from pairs of males were fed until after the second observation session (16–17 days later), when the feeder was removed. Seventeen days later, there was a third observation session. For each supplemented

male, there was a control male that was observed on the same mornings, and empty feeders were also provided in the territories of control males. We observed one pair of supplemented and control males per morning. The first observation session in a given territory took place between 7 and 27 March. The second observation session took place between 24 March and 13 April, that is, between 33 and 8 (mean \pm SE = 21 \pm 1.4) days before the first egg was laid by the female (supplemented males: 22 \pm 2.0 days before first egg; control males: 20 \pm 2.0 days before first egg; Student's *t* test: $t_{18} = -0.89$, $P = 0.38$; for egg-laying dates see the Results). The third observation session took place between 10 and 30 April, that is, between 16 days before and 9 days after the first egg was laid by the female (supplemented males: 5 \pm 2.2 days before first egg; control males: 3 \pm 2.0 days before first egg; Student's *t* test: $t_{17} = -0.89$, $P = 0.38$). Supplemented males were fed ad libitum, using commercially available sunflower seeds and wild bird fat balls. The feeder containing the sunflower seeds was hanging from a tree about 5 m from the tree supporting the nestbox, at a height of about 1.5 m, and was replenished every other day so that it always had some food in it. The fat balls were hanging in bushes next to the feeder.

Song recordings started 1 h before sunrise and continued until 1 h after sunrise (sunrise times taken from www.sunrisesunset.com for Oslo, Norway). Recordings were made using Sony TC-D5 Pro II tape recorders and Telinga parabolic microphones. We also noted exact starting times of dawn singing and the number of other great tit males intruding into the territory. Great tits usually sing strophes lasting 1–5 s, and after a strophe, they pause a few seconds before a new strophe begins (Lambrechts 1997). We measured song output as the sum of all strophe lengths in seconds (Gorissen et al. 2005), that is, the total time a bird was singing during the 2 h of song recording. Strophe lengths were measured using the software SyrinxPC, version 2.6h (J. Burt, www.syrinxpc.com).

We used linear mixed-effects models (LMM, function `lme`, package `nlme`; Pinheiro et al. 2009) in R 2.9.1 (R Development Core Team 2009) for analysing the starting time of dawn singing and song output. We used generalized linear mixed-effects models (GLMM, function `glmer`, package `lme4`; Bates & Maechler 2009) with logit link function and binomial error distribution for analysing whether or not a bird was singing, and GLMM with log link function and Poisson error distribution for analysing numbers of intruders. The significance of the predictor variables was assessed using likelihood ratio tests. For all likelihood ratio tests, the degrees of freedom were $df = 1$. As fixed factors, we included treatment (supplemented male versus control) and observation session (second versus third session). We further included age (yearling versus older) in the model on whether or not a bird was singing, and starting time of dawn singing (minute during the 2 h of observation) in the model on song output. In all models, we also included the interaction between treatment and observation session; nonsignificant interactions were then removed from the models. Song measures from the first observation session were included as a covariate. Individual subject nested in matched pair (supplemented male and its control) was included as a random factor, to account for the repeated sampling of the same individuals, and thus the nonindependence of data points. We visually checked homogeneity of variance and normality of error using plots of standardized residuals against fitted values and of quantiles of residuals against quantiles from a normal distribution.

Our study was conducted under licence from the Directorate for Nature Management in Norway.

RESULTS

All males were paired during the study period, but the females of eight males (three supplemented birds, five controls) were not

observed to lay eggs at the study site. Of the remaining birds, the females of supplemented males ($N = 11$) started laying eggs between 17 April and 4 May (mean \pm SE = 25 April \pm 1.6 days), while the females of control males ($N = 9$) started laying eggs between 17 April and 28 April (22 April \pm 1.1 days). However, the difference in laying dates between the two groups of males was not significant (Student's t test: $t_{18} = -1.7$, $P = 0.11$). Clutch sizes were 6–12 eggs (8.6 ± 0.54) for supplemented males ($N = 11$) and 5–10 eggs (8.1 ± 0.54) for control males ($N = 9$); the difference in clutch sizes was not significant ($t_{18} = -0.7$, $P = 0.51$).

In 12 individual second or third observation sessions, from 11 subjects (five supplemented birds, six controls), the male did not sing, although it was present in its territory. In two additional observation sessions (one supplemented bird, one control), the male was not found in its territory. Neither the treatment nor the observation session, nor their interaction, significantly predicted whether a male was singing or not (GLMM: all $P > 0.16$). However, yearling males had a lower probability of singing (0.57) than older males (0.83; likelihood ratio (LR) = 16.56, $P < 0.001$). In the following analyses on starting time of dawn singing, we omitted individual observation sessions in which the male did not sing or was not found in its territory, leading to sample sizes for the second and third observation sessions of $N = 10$ and 12 for supplemented males and $N = 9$ and 11 for control males. Because, after this, only six observation sessions for yearling males were left in the data set, we ignored the factor age in all further analyses (which did not importantly change the results).

Supplemented males started to sing later relative to sunrise than control males (LMM: LR = 4.22, $P = 0.039$; Fig. 1). In 36% of observation sessions, supplemented males started to sing only after sunrise and thus skipped their regular dawn singing (10% in controls). Both the supplemented and control males started to sing earlier during the third observation session than during the second session (LR = 6.44, $P = 0.011$; Fig. 1). The interaction between treatment and observation session was not significant (LR = 0.07, $P = 0.79$), suggesting that the later start of dawn singing in

supplemented males during the second observation session was carried over to the third observation session (Fig. 1).

In the following analyses on song output (sum of all strophe lengths during 2 h), we omitted individual observation sessions in which the male was not found in its territory or in which song recording failed because of technical problems, leading to sample sizes for the second and third observation sessions of $N = 13$ and 12 for supplemented males and $N = 14$ and 13 for control males. We did not find that treatment or the interaction between treatment and observation session predicted song output (LMM: both $P > 0.79$; Fig. 2). Also, starting time of dawn singing did not predict song output during the 2 h (LR = 0.61, $P = 0.43$). However, supplemented males and controls sang more during the third observation session than during the second (LR = 5.01, $P = 0.025$; Fig. 2).

During the 2 h of song recordings, we observed 3.1 ± 0.3 conspecific male intruders in the territory of a subject, but the numbers of intruders did not differ significantly between treatments or observation sessions (GLMM: main effects and interaction: all $P > 0.11$). During the second observation session (which was the last morning that food was provided in a territory), we never saw a great tit feeding at the feeder before sunrise. One hour after the second observation session, we observed the feeding stations for 30 min. During this time, there were 0.6 ± 0.4 conspecific male intruders feeding at the feeder, while the territory owner was seen feeding at the feeder on 1 ± 0.3 occasions. We observed 2.6 ± 0.9 individuals of other bird species at the feeder (mostly blue tits, nuthatches, *Sitta europaea*, greenfinches, *Carduelis chloris*, blackbirds and great spotted woodpeckers, *Dendrocopos major*).

DISCUSSION

After 2 weeks of supplementary feeding in the territories of great tits, supplemented males started dawn singing later than control males. Great tits usually start singing well before sunrise during at least 6 weeks before egg laying (Amrhein et al. 2008); our supplemented males, however, on average started to sing around sunrise and thus postponed singing at dawn. Despite a later start of dawn singing, however, supplemented males did not have

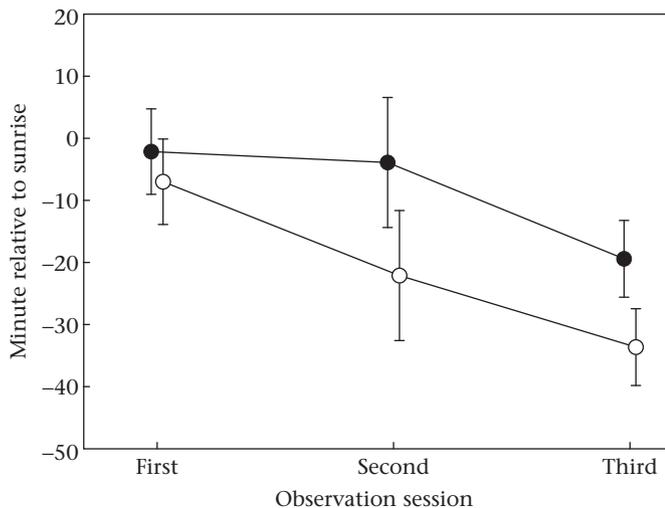


Figure 1. Mean \pm SE start of dawn singing in minutes relative to sunrise, in 14 food-supplemented male great tits (filled circles) and in 14 control males (open circles). There were 16–17 days between the first and the second, and between the second and the third observation sessions. From immediately after the first observation session until after the second observation session, supplemented males were supplied with sunflower seeds and wild bird fat balls in their territories. Individual observation sessions in which a male did not sing or was not found in its territory were deleted, so that sample sizes for the first, second and third observation sessions were $N = 14$, 10 and 12 for supplemented males and $N = 12$, 9 and 11 for control males.

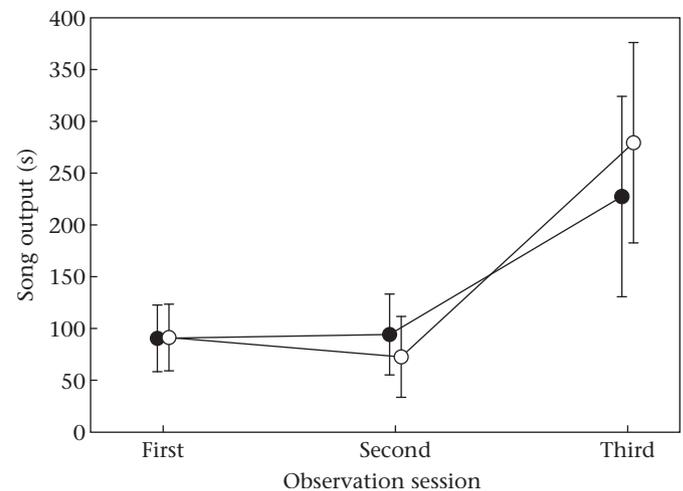


Figure 2. Mean \pm SE song output during 2 h in seconds (sum of all strophe lengths 1 h before and 1 h after sunrise), in 14 food-supplemented male great tits (filled circles) and in 14 control males (open circles). Individual observation sessions in which a male was not found in its territory or in which song recording failed because of technical problems were deleted, so that sample sizes for the first, second and third observation sessions were $N = 13$, 13 and 12 for supplemented males and $N = 12$, 14 and 13 for control males.

a significantly different song output from control males in the 2 h around sunrise. The later start of singing in supplemented males was maintained for 2 weeks after food supplementation had ended. Our results show that great tits that are being fed until about 3 weeks before the start of egg laying may postpone their regular dawn singing before sunrise for extended periods of time.

The delaying effect of feeding on the start of dawn singing was surprising, because, as predicted by formal models (McNamara et al. 1987; Hutchinson et al. 1993; Hutchinson 2002), field studies using short-term food supplementation for 1–5 days reported an earlier start of dawn singing or a higher dawn song output (Cuthill & Macdonald 1990; Barnett & Briskie 2007; Grava et al. 2009). Studies using long-term food supplementation mainly looked at singing during the day and not at dawn, and almost always found an increase in song output (Thomas 1999). Similarly to our study, however, Clarkson (2007) found that during the breeding season, and in comparison with unsupplemented birds, migratory prothonotary warblers, *Protonotaria citrea*, sing less frequently at dawn 2 weeks after long-term food supplementation has ended. It is currently unclear why the effects of long-term food provisioning on dawn singing of songbirds seem to contrast sharply with the effects of short-term food provisioning. In the following, we discuss possible causes and consequences of the finding that regular wild bird feeding delays the start of dawn singing.

Kacelnik (1979) suggested that, at dawn, great tits spend their time singing because at low light levels, hunting for insects is less profitable. Food from feeders may be easily obtained at twilight, so our subjects could have delayed dawn singing because they were foraging; however, during our second observation session we never observed a great tit at the feeder before sunrise. Furthermore, birds may change their dawn singing during long-term food supplementation because they suffer from greater conspecific intruder pressure (Cuthill & Macdonald 1990; Berg et al. 2005); however, we did not observe more great tit intruders at dawn in the territories of supplemented males. Because the feeding stations also attracted other bird species, it is possible that heterospecific intruders had some influence on song output as well. Independently of intruder numbers, though, supplemented males may have shifted from an energetically relatively inexpensive territory defence behaviour (singing) to a more costly defence behaviour (chasing intruders; Ewald & Carpenter 1978). Indeed, Ydenberg (1984) showed that great tits with access to supplementary energy sources responded to simulated intruders by attacking them more than controls did, but not by singing more. A long-term effect of food supplementation beyond the end of food provisioning could then be explained by higher energy reserves of supplemented birds, or by a different perception of the value of the territory (Thomas 1999).

However, other and nonexclusive explanations for the long-term effect on dawn singing are possible; for example, if there are additional feeders available in the neighbourhood, birds that were formerly supplemented within their territory may simply continue relying on human-provided food from other sources. Also, the quality of the supplementary food itself could influence the territorial behaviour of birds, because supplemented great tits, rather than hunting for insects, might rely solely on the commercial food provided at the feeder. Furthermore, supplemented birds could delay their start of dawn singing because lasting concentrations of birds at feeders may attract predators (Krams 1998), and singing could attract the attention of those predators (Lima 2009). Sparrowhawk, *Accipiter nisus*, and pygmy owl, *Glaucidium passerinum*, which are considered to be the most important airborne predators of tits in Northern Europe (Krams 2000), are both present at our study site (T. Slagsvold, unpublished data). Although no pygmy owls were seen during the present study, singing during the dawn chorus might be particularly risky, because the mainly

crepuscular pygmy owl and the more diurnal sparrowhawk may be hunting simultaneously at dawn (Krams 2000; Lima 2009). We would not necessarily expect, though, that predation risk would be increased for 2 weeks after food supplementation has ended, and thus this is unlikely to explain the long-term effect on dawn singing that we found in our study.

Egg-laying dates and clutch sizes did not differ significantly between supplemented and control territories. However, supplementary feeding could still affect the reproductive success of males by influencing extrapair behaviour of the females. Female songbirds soliciting extrapair copulations from neighbouring males may be allowed to feed on neighbouring territories (Gray 1997). Females that receive supplementary feeding within their own territory may thus show less inclination towards seeking extrapair copulations. Accordingly, if the dawn song of male great tits were a paternity guard (Mace 1987), males in supplemented territories might delay dawn singing because their paternity is less at risk. Furthermore, supplemented males could gain extrapair paternity by soliciting females visiting their territories to feed. However, supplementary feeding could also have detrimental effects on male paternity. Female songbirds may base their extrapair mating decisions on male song characteristics such as song repertoire or song length (Hasselquist et al. 1996; Gil et al. 2007) or on male performance during vocal interactions (Mennill et al. 2002). If food-supplemented male great tits delay dawn singing for some reason unrelated to female behaviour, their females might be attracted by extrapair males that are singing at dawn, potentially leading to paternity loss for the supplemented males.

We conclude that feeding may not only help wild birds survive the winter but may also change their territorial behaviour in a longer-lasting way. In our study, we used four significance tests on the same data to test our hypothesis that wild bird feeding affects dawn song performance (treatment main effects and interactions for starting time of dawn singing and for song output). Following Gelman & Hill (2007), we accept that multiple tests on the same hypothesis will be mistaken on occasion (as applies for significance tests in general). We believe that the only way to provide strong support for a hypothesis is independent replication of the experiment, which we would like to encourage. Clearly, more research on long-term supplementary feeding is needed that takes into account the changes in spatial behaviour of supplemented males both inside and outside their territories, the behaviour of females, and the possible influence of predators. Our study showed that providing supplementary food to great tits from about 5 weeks until 3 weeks before the start of egg laying delayed dawn singing for at least 2 more weeks until egg laying actually began. Being in sharp contrast to results from short-term supplementation studies, our findings suggest that the duration of an experimental manipulation of food availability is of critical importance. As Jones & Reynolds (2008) put it, the worldwide practice of wild bird feeding may be seen as a large-scale supplementary feeding experiment. We recommend that behavioural ecologists continue studying the effects of this large-scale feeding effort using controlled experiments manipulating food supply on the small scale.

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