

Wild bird feeding (probably) affects avian urban ecology

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3.1 Introduction

Why do people feed wild birds? It is intuitively clear that humans feel delighted by the presence of birds that they can manage to attract by offering ordinary seeds at a feeder. According to surveys on human motivations for feeding wild birds in Australia, some people may gain experiential knowledge from observing the birds in their gardens, or feed the birds in return for the massive habitat destruction caused by humans (Howard & Jones, 2004; Ishigame & Baxter, 2007). However, outside Australia, the largely unstudied motivations of people feeding birds are just one example for our gaps of knowledge with respect to bird feeding (Jones & Reynolds, 2008).

It is in sharp contrast to our limited knowledge on the habit that wild bird feeding is probably the most widespread and popular form of human–wildlife interaction throughout the world (Jones, 2011), and, at least in northern temperate regions, the largest wildlife management activity (Martinson & Flaspohler, 2003). In the UK, sufficient commercial wild bird foods are sold to support a hypothetical number of over 30 million great tits (*Parus major*; Robb et al., 2008a), which is many more than the 2 million pairs of great tits that are actually present (www.bto.org). Surveys have found that 64% of households provide supplementary food for birds in the UK (Davies et al., 2012), and 43% in the USA (Martinson & Flaspohler, 2003). In suburban and rural environments of Australia, estimated household feeding rates range from 36% to 48% (Ishigame & Baxter, 2007). Although Bird-Life Australia does not encourage supplementary

feeding of wild birds (Bird Observation and Conservation Australia, 2010), northern organizations such as the British Trust for Ornithology (BTO), the Royal Society for the Protection of Birds (RSPB) and the Cornell Laboratory of Ornithology now recommend feeding birds for promoting nature conservation (Jones, 2011). In Germany, a renowned ornithologist recently wrote a popular book on bird feeding that sold 50,000 copies in the first 1.5 years, in which he advocates feeding the birds year-round and on a massive scale (Berthold & Mohr, 2008). Indeed, wild bird feeding is not only here to stay (Jones, 2011), it also seems to be increasing, at least in the UK (Chamberlain et al., 2005).

Today, in many countries, the huge effort in providing supplementary food for birds may be one of the largest human influences on bird populations, in addition to habitat loss and change, human-induced climate change and hunting. As I will show in this chapter, we now have a sound basis of knowledge about the impacts that supplementary feeding can have on birds. However, as I will also show, our knowledge mostly comes from small-scale experiments that researchers did in natural and rural habitats. Surprisingly little is known on the impact of feeding birds in our urban gardens and backyards. However, humans are influencing urban food supply for birds not only directly by providing feeders, but also via waste treatment and by creating, changing, or destroying urban or natural habitats and food sources in our cities (Chace & Walsh, 2006). Because such additional human influences are usually weaker in rural landscapes, the effects of feeding wild birds are likely

to differ between natural study sites and urban environments.

In this chapter, I will highlight important findings on the effects of food supplementation on avian ecology. Food supply clearly influences bird numbers both in winter and during the breeding season (Martin, 1987; Newton, 1998), and feeding short-lived passerines can alter almost every aspect of their ecology, from reproductive parameters to behaviour and distribution (Martinez-Abraín & Oro, 2010). Because providing supplementary food is so easily done, manipulating food supply was a method of choice in many areas of research. Throughout, I will distinguish between results obtained from rural or natural study sites and from studies in urban habitat. At several places, I will point to study questions and methods that I think would be worth considering. Finally, I will discuss possible reasons why there is so little research on bird feeding in cities and give examples what could be done to change that.

3.2 Body condition and survival

The most obvious reason why people provide supplementary food for birds in winter is probably that they hope to enhance body condition of the birds to help them survive.

As expected, wild bird feeding appears to affect body condition. In Ohio, supplementary food improved the nutritional condition of wintering woodland birds, as indicated by the faster daily growth rates of feathers of provisioned birds than of unprovisioned birds (Grubb & Cimprich, 1990). Australian magpies *Cracticus tibicen* receiving supplementary food had a higher body mass, and when supplied with sausages, they also had higher plasma cholesterol levels (Ishigame et al., 2006). It seems that birds may often gain higher body mass when receiving supplementary food in natural habitats (Boutin, 1990), but this may not always be found to a similar degree in urban habitats: when Liker et al. (2008) kept house sparrows in aviaries under *ad libitum* food supply, urban sparrows had a consistently lower body mass than sparrows from rural origin, which the authors explain by habitat differences in nestling development or by adaptive divergence of sparrow populations. This is clearly calling for more studies comparing how wild bird

feeding affects body condition in urban and rural areas.

In one of the first reviews on food supplementation experiments under field conditions, Boutin (1990) states that survival over the winter and subsequent breeding density has been the focus of most food addition studies. Survival rates were improved in all of the six reviewed cases where survival was measured (Boutin, 1990). For example, black-capped chickadees *Poecile atricapillus* with access to winter food had much higher over-winter survival rates than birds on control sites (69% vs. 37%; Brittingham & Temple, 1988). In all six studies, however, supplementary food was provided in rural and natural forests and not in urban areas. In one of the few studies in urban landscapes, Egan and Brittingham (1994) found that black-capped chickadees had higher monthly survival rates (94%) in a suburban area with mature trees and bird feeders throughout than in mature forests without supplementary food provision (81%). However, the authors suggest that feeders probably influenced movements of the birds and that greater apparent survival was measured rather than actual survival; thus, the birds may have been more closely attached to a study site when food was provided, and feeding could have reduced emigration rather than have enhanced survival. As is often the case, it is difficult to distinguish between emigration from a study site and actual death in food supplementation studies, unless the degree of dispersal is estimated and accounted for; this could be done by capturing at multiple neighbouring plots (Marshall et al., 2004) or by using radio telemetry (Sandercock, 2006).

I suggest studying winter dispersal for estimating true survival in urban habitats in which supplementary food is provided, and to compare this with control sites without bird feeders in similar urban habitat and in rural landscapes. Because urban habitats are often highly heterogeneous, it would be particularly advisable to randomly select fed and unfed urban sites and then to swap these over between years to try and control for habitat differences. Dispersal and true survival could be estimated by capturing individuals in several gardens within an urban area. To account for the degree of dispersal that is likely to be a function of the distance between study plots, distances between capture sites

should be varied, but capture sites should be within potential reach for dispersing subjects. It should also be possible to study the movements of supplemented birds in urban landscapes by using radio telemetry in winter.

3.3 Density and distribution

Immigration, emigration, and survival determine how effects of winter feeding carry over to influence bird density during the next breeding season. Newton (1998) reviewed studies that experimentally manipulated food supply to investigate changes in bird numbers. He found 15 cases in which extra winter food provision was followed by an increase in subsequent breeding density by a factor ranging from 1.2 to 2.4, while in 11 cases, there was no clear increase. Although those numbers include some results that are not strictly independent because they are from different species investigated during the same studies, it appears that winter feeding can enhance breeding density by increasing survival or immigration, or by reducing emigration. A mechanism leading to higher bird numbers could be that supplementary feeding influences breeding density by affecting territorial behaviour. For example, if males reduce the size of their territories when supplementary food is provided (Enoksson & Nilsson, 1983), density of territories could be increased, which again calls for studies combining supplementary feeding with radio telemetry.

Often, winter food supplementation affects breeding numbers only when natural food supply is poor; for example, van Balen (1980) found that in great tits, supplementary feeding almost doubled the number of breeding pairs in years of poor beech *Fagus sylvatica* crop, but had little impact in years with good beech crop. Generally, of course, many factors will contribute to variation in the effects of food supplementation found between studies. For example, long-lived species that often inhabit the same breeding territories for several years may show less sudden increases in density after supplementary feeding than short-lived species (Newton, 1998); also, studies using short time periods of experimental food provision are likely to yield different outcomes than studies providing supplementary food for longer periods (Harrison et al., 2010; Newton,

1998; Saggese et al., 2011). Results are clearly most valuable if they come from long-term studies evaluating potential effects of inter-year variance in environmental conditions (Schoech, 2009).

The studies reviewed by Newton (1998) are generally from natural habitats. In urban areas, post-winter densities of Carolina wrens *Thryothorus ludovicianus* were predicted by the presence of bird feeders (Job & Bednekoff, 2011). Data from the BTO Garden Bird Feeding Survey showed that several species are positively associated with the number of feeding stations provided by survey participants (Chamberlain et al., 2005). In the city of Sheffield, the density of feeding households was positively related to bird abundance (Figure 3.1), but had no apparent effect on overall species richness; however, in an individual garden, wild bird feeding will almost always increase the range of species and the number of individuals (Fuller et al., 2008). The studies cited above are all correlational, and, so far, no experiment manipulating food supply for investigating effects on bird density and distribution has been reported from an urban environment.

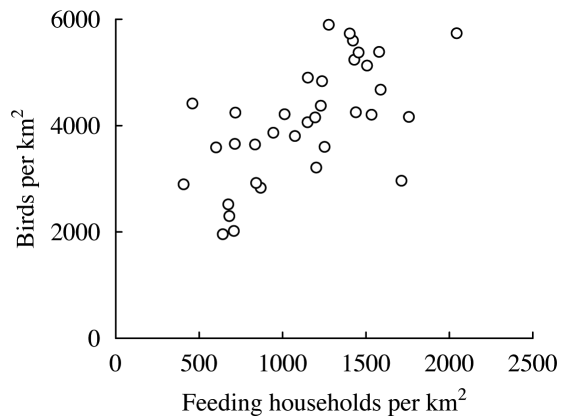


Figure 3.1 Relationship between bird abundance and levels of bird feeding in 35 neighbourhood types, summarized from 160 1-km squares with 442 bird survey points spread across urban Sheffield (UK). Points are mean values per km², calculated from the survey points falling within each neighbourhood type. Abundance is the mean number of individuals of all bird species per km² calculated using distance sampling. The density of households providing food for wild birds was a strong predictor of bird abundance in the urban landscape after accounting for the effect of cover by greenspace. Data are from Fuller et al. (2008), with kind permission by the authors.

On a larger scale, wild bird feeding may be partially responsible for northward range expansions, for example of the northern cardinal *Cardinalis cardinalis* and the American goldfinch *Carduelis tristis* in the USA (Robb et al., 2008b). In Europe, a rapid evolution of a new migratory divide has been observed in blackcaps *Sylvia atricapilla* that since the 1960s have established winter quarters in Britain, 1000 to 1500 km north of their traditional wintering areas. Among other factors such as climate warming, improved wintering conditions in Britain due to wild bird feeding may have contributed to this development (Bearhop et al., 2005, Berthold et al., 1992).

3.4 Productivity

In his review, Boutin (1990) noted that few studies have examined the effect of food supplementation on reproductive success in birds. Today, however, reproductive performance is probably the most widely researched topic in studies on food supplementation, as indicated by the 59 studies reviewed by Robb et al. (2008b) that provide data on how food supplementation influences the dates of egg laying.

In 58% of those 59 studies, feeding led to significantly earlier laying dates (Robb et al., 2008b). An increase of either clutch size, hatching success, chick growth rate, or fledging success due supplementary food was found in 44% to 64% of studies, and while between 36% and 55% of studies found no significant effect of supplementary feeding on a particular measure of breeding success, only three studies found negative effects on one of the measures (Robb et al., 2008b). It thus seems well established that providing supplementary food often enhances productivity of birds.

One recent study producing mixed evidence was by Harrison et al. (2010), who found that while supplementary feeding advanced laying in blue tits *Cyanistes caeruleus* and great tits, brood size at hatching was reduced by about half a chick in both species. The authors speculate that the provided peanut cakes may have led to smaller clutch sizes due to their high contents of fat rather than of protein; however, they note a striking similarity of their results from a natural woodland to urban habitat, in which often food is provided throughout the year,

and in which both species of tits usually lay smaller clutches than in natural habitats (Chamberlain et al., 2009). Unlike other studies that often provided food for relatively short periods of time, Harrison et al. (2010) supplied bird food continuously from several weeks prelaying until hatching of the young, thus more closely mimicking how food is provided during the breeding season in an increasing number of urban gardens in which birds are fed year-round (Jones & Reynolds, 2008). However, the authors note that also other factors in addition to supplementary feeding may influence reproductive parameters of urban birds, and that although logistically challenging, further research in urban garden habitats would clearly be of value (Harrison et al., 2010). Indeed, the only way to study the effects of wild bird feeding on productivity while controlling for additional urban influences is probably to compare birds that do have access and that do not have access to bird feeders in otherwise similar urban landscapes.

Again, most studies on productivity have been conducted in natural habitats so far, and we are generally lacking information on how food supplementation affects reproductive performance of birds breeding in our gardens. This is exemplified by a brief survey of the 56 studies that Robb et al. (2008b) list in the electronic Appendix of their review. Of those 56 studies dealing with various impacts of supplementary feeding on breeding success, only four were carried out in urban habitat, and one was in suburban habitat. The only study on a non-corvid urban passerine was by Crossner (1977) on European starlings *Sturnus vulgaris* breeding in nestboxes on a university campus. The other urban studies were, again on a university campus and in other urban habitat, by Hochachka and Boag (1987) and Dhindsa and Boag (1990) on the black-billed magpie *Pica pica* and by Richner (1992) on the carrion crow *Corvus corone corone*, and, in suburban habitat, by Schoech et al. (2004) on the Florida scrub-jay *Aphelocoma coerulescens*. The other 49 studies were done in natural habitat outside residential areas, and two studies were on zebra finches *Taeniopygia guttata* in the laboratory. Thus, most of our knowledge on the influence of wild bird feeding on reproductive performance of city birds comes from outside cities, or from corvid species

within cities. A subtle preference by researchers for corvids such as magpies and crows may be explained by the often easily visible nests alongside public roads. In natural habitats, many if not most published experiments using supplementary food provision were done on tits in forest nestbox-plots (Newton, 1998), and we have yet no information on how urban birds breeding in nestboxes are dealing with the bird feeders that are often found in close proximity to their nestboxes.

Further, most studies on the influence of artificial food supply on reproductive performance provided supplementary food during the breeding season. Although city birds are now often fed well into the breeding season or even year-round (Jones & Reynolds, 2008), most wild bird feeding is still being done in midwinter (Chamberlain et al., 2005). Only two studies seem to have investigated how food supplementation that is restricted to the winter season carries over to influence reproductive performance during the breeding season: Robb et al. (2008a) found that feeding that stopped 6 weeks prior to laying advanced laying dates and increased fledging success in the blue tit. Plummer et al. (2013) reported that provision of fat during winter resulted in smaller relative yolk mass in larger eggs and reduced yolk carotenoid concentrations in early breeding blue tits. This suggests that at least when the nutritional composition of provisioned foods is reduced to vegetable fat, carry-over effects on breeding performance may not always be beneficial (Plummer et al., 2013).

3.5 Song and territorial behaviour

A number of studies showed that supplementary feeding enhances territory defence activity. Ydenberg (1984) placed feeding tables in the territories of great tits and then simulated territorial intrusions using song playback and a stuffed mount of a male. He found that males with access to a feeding table attacked the model more than males who received no extra food. Ydenberg and Krebs (1987) then suggested that supplementary food allowed the birds to invest more time in territorial activity by allowing them to meet their food requirements more rapidly. Also, foraging temporally conflicts with singing (Gil & Gahr, 2002), and song output

of male songbirds is likely to be constrained by energy reserves (Berg et al., 2005). Accordingly, eight of nine studies that were reviewed by Thomas (1999) found that food-supplemented males increased song output.

A particularly sensitive time of singing is during the dawn chorus in the hour before sunrise. In some species, dawn singing seems to be important for territory defence (Amrhein et al., 2004; Slagsvold et al., 1994), and studies on the winter wren *Troglodytes troglodytes* found that the number of songs sung before sunrise reflect past territorial intrusions by conspecific males more clearly than singing after sunrise (Amrhein & Erne, 2006; Erne & Amrhein, 2008).

Studies providing supplementary food for 1 to 5 days found an earlier start of dawn singing or a higher dawn song output in the blackbird *Turdus merula* (Cuthill & Macdonald, 1990), the silvereye *Zosterops lateralis* (Barnett & Briskie, 2007), and the black-capped chickadee (Grava et al., 2009). However, wild birds are usually fed over much longer periods, which will influence other variables that in turn will affect song output in complex ways (Thomas, 1999). For example, wild bird feeding may attract conspecific males into the territory of a supplemented male (Berg et al., 2005; Cuthill & Macdonald, 1990; Davies & Houston, 1981; Tobias, 1997), and Ydenberg (1984) and Tamm (1985) found that higher intruder pressure due to supplementary feeding leads to more chasing and attacking, but not to more singing or display activity by the territory owner.

We studied how a longer period of feeding would affect dawn singing of great tits in an extensive nestbox-plot near the city of Oslo (Saggese et al., 2011). Supplementary food was provided for 16 or 17 days *ad libitum* within the territories, starting about 5 weeks before the first egg was laid in a given territory. We found that by the end of the feeding period, supplemented males started to sing later relative to sunrise than control males (second observation session in Figure 3.2). Further, the later start of dawn singing carried over to a third observation session, 17 days after supplementary feeding had ended (Figure 3.2). This suggests that supplementary feeding had long-term effects on behaviour beyond the end of food provision (for

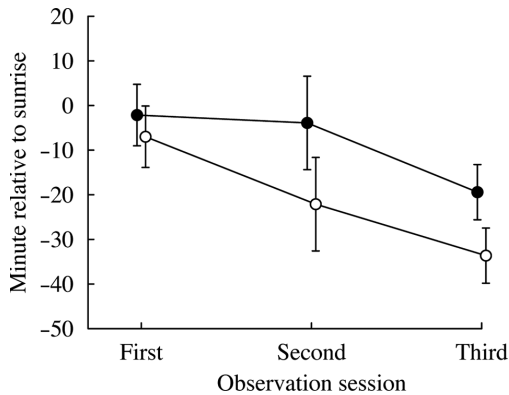


Figure 3.2 Mean \pm SE start of dawn singing in minutes relative to sunrise, in 14 food-supplemented male great tits (filled circles) and in 14 control males (open circles). There were 16–17 days between the first and the second, and 17 days between the second and the third observation sessions. From 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. Data are from Saggese et al. (2011).

details, see Saggese et al., 2011). Our results contrast with those from studies using shorter periods of food supplementation (Barnett & Briskie, 2007; Cuthill & Macdonald, 1990; Grava et al., 2009) in that we found a later, not an earlier start of dawn singing in supplemented birds. Similarly to our study, however, Clarkson (2007) found that 2 weeks after long-term food supplementation had ended, supplemented prothonotary warblers *Protonotaria citrea* sang less frequently at dawn in comparison with control birds.

These examples suggest that to investigate realistic effects of wild bird feeding as practised in urban gardens, food needs to be regularly provided for longer periods of time, which may lead to results that differ from what we know from short-term supplementation studies. Needless to say that none of the studies cited in this paragraph investigated territorial and singing behaviour within urban residential areas.

In general, future research could focus on how supplementary feeding influences distribution and reproduction via effects on social interactions. Further,

although studies have shown that birds feeding at feeders may not bear a higher risk of predation, wild bird feeding could affect distribution and behaviour of both predator and prey species (Robb et al., 2008b; Saggese et al., 2011). We certainly need more food supplementation studies that take a behavioural point of view, because the mechanisms behind changes in survival, distribution, and productivity are far from being understood (Jones, 2011). Because resident birds may form pairs already in winter (e.g., Lemmon et al., 1997), changes in singing and territorial behaviour that are caused by food supplementation within the territory of a male during winter likely affect pair bonding and later reproductive performance.

3.6 Conclusion

In the urban backyards and gardens of the world, there are millions of bird feeders alongside millions of nestboxes. From what we know about the effects of supplementary feeding in rural and natural areas, it seems clear that wild bird feeding heavily influences multiple aspects of avian urban ecology. To date, however, we have little published information on the influence of wild bird feeding on reproductive performance of city birds. Further, there are hardly any experimental studies on how manipulated food supply in our cities affects survival, dispersal, distribution, and behaviour of birds. Why is that so? Of course, the problem about private gardens is that they are private. But if we want to learn how wild bird feeding affects avian urban ecology, we must learn to avoid the natural settings and seek out garden habitats.

We certainly know a lot about how supplementary feeding affects different aspects of avian ecology from many well-designed experiments performed in natural and seminatural study sites. However, in our cities, birds have greater access to anthropogenic foods of all sorts, while access to insects and other natural food resources may be reduced (Chace & Walsh, 2006). Environmental cues and species assemblages are so different in urban and rural areas that for many bird species, the effects of wild bird feeding probably differ between urban, suburban, and rural areas. However, even for such a basic statement, it is hard to find any reference.

It is clear that studies using experimental manipulation of food supply in urban areas will pose a much greater logistical challenge than studies in easily accessible rural nestbox-plots where food supplement availability is relatively easily controlled, and where habitat may be broadly homogeneous. In contrast, urban habitats seem to be characterized by small-scale variation in environmental factors that include differences in vegetation and natural food resources from garden to garden.

However, why not make use of this small-scale variation, by investigating several smaller study plots rather than a large one, perhaps with the help of voluntary nest recorders and bird ringers in city gardens? It should be possible to convince interested garden owners to put up new bird feeders, for the sake of a scientific experiment. It may also be possible to convince already keen bird feeders to stop feeding in their gardens, and maybe in some neighbouring gardens, at least for restricted periods of time. Using such local food deprivation or supplementation, future studies could compare multiple scattered urban study plots rather than investigating one continuous area as has usually been done in experiments from non-urban study sites. On such local urban study plots, one could then differentially vary, for example, the quantity of food supply or the lengths of food provision periods, to highlight multiple research questions such as the contested issue whether wild birds should be fed only in winter or year-round (Berthold & Mohr, 2008; Jones & Reynolds, 2008).

To study how wild bird feeding affects avian urban ecology, most of the research discussed in this chapter should be replicated in urban environments. Conducting research on bird feeding ecology in our cities is probably not for the faint-hearted (Jones, 2011); but it is urgently needed and a promising new field for adventurous scientists.

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