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Wild bird feeding is one of the most common forms of human-wildlife interactions in the Western world. Originally a practice providing nutritional assistance to over-wintering birds, especially in more northern latitudes, birds throughout the cities of the world are now provided with considerable amounts and a variety of foods year-round. Despite the global nature of the practice, remarkably little is known about the outcomes and implications of what may be seen as a supplementary feeding experiment on a massive scale. Although many claims are made about the benefits of feeding, there are growing concerns about the spread of disease, poor nutrition, risk of dependency and many other important issues. Constructive debate among increasingly vigorous proponents and opponents is currently constrained by a lack of reliable information. Here we argue that bird feeding provides an important, if challenging, opportunity for fundamental research in urban ecology.

Every day, throughout the Western world, householders place seeds, sugar mixtures, food scraps and meats on trays and in hanging feeders, as supplementary food sources for wild birds. Whether to ameliorate poor foraging conditions, to monitor species richness and abundance, or simply to enjoy the presence of otherwise free-living wildlife, many people are passionate participants in the supplementary feeding of wild birds (Dunn and Tessaglia-Hymes 1990, Cannon 2000, Howard and Jones 2004). Participation rates are consistently high across the Western world: percentages of households providing food for birds at some time have been estimated at 43-50% for the United States (Deis 1988, Geis and Pomerey 1993, U.S. Dept. Interior and U.S. Dept Commerce 1997, Rogers 2002), 34-75% for the United Kingdom (Cowie and Hinsley 1988) and 38-57% for Australia (Rollinson et al. 2003, Howard and Jones 2004), with up to half of these doing so daily (Rollinson et al. 2003, Chamberlain et al. 2005).

By a range of measures, it is an activity operating on a large scale. In the US alone, recent estimates indicate that over 82 million people are involved, purchasing over 450 million kg of seed at a cost of about US$3.5 billion each year; a further US$730 million was spent on feeders and related hardware (U.S. Dept. Interior, Fish and Wildlife Service 1998, 2002). Comparable figures for elsewhere are not readily available but it is estimated that US$440 million and US$220 million are spent annually on supplementary food in the UK and in mainland Europe, respectively (CJ Wildlife pers. comm.). While providing small amounts of food to attract wild animals has probably been a feature of human settlements for millennia (Kellert 1997), it is only during the last few decades that the feeding of birds has become widespread with a concordant growth of allied industries (seed, feeders, guidebooks etc.) (Peterson 2000, Chinery 2004).

Feeding has traditionally been a winter activity, which probably started as humane assistance for malnourished birds during harsh Northern Hemisphere seasons (Dunn and Tessaglia-Hymes 1990, Brittingham 1991, Kress 1998). This probably remains the predominant practice in many parts of the US and UK, but it is now also commonly practiced year-round, with many feeders replenished daily throughout the year (Cannon at al. 2005). Indeed, considerable effort is now being expended to convince the more traditional 'winter-only' participants that year-round feeding is both appropriate and beneficial to wild bird populations, aiding survival and enhancing reproduction (Anon. 2004).

The role of food quality and availability in the ecology of animals is a well-researched field (see review by Boutin 1990) and the provision of supplementary foods is established as an experimental method for the study of the influence of food on the behaviour and condition of a broad range of taxa (The Wildlife Society 2007). Supplementary feeding has also been used as a wildlife management technique to enhance the survival and reproductive success of species (e.g., Castro et al. 2003, Gonzalez et al. 2006, Houston et al. 2007), to concentrate animals for observation and hunting (Dunkley and Cattet 2003), to assist in monitoring disease, and to reduce predation on target species by provisioning predators (The Wildlife Society 2007).

Many supplementary feeding experiments have shown that even moderate amounts of additional foods can profoundly influence reproductive outcomes of the target species (e.g., see reviews by Boutin 1990, Christians 2002). The majority of these studies show that increasing the available food resource advances the onset of reproduction, prolongs the breeding period and increases the number of young produced per year (Boutin 1990). In some bird species, more food also results in more offspring per breeding attempt (e.g., Schoech 1996). More recently, researchers have started to investigate the influence of specific aspects of the nutritional components of diets, including the importance of protein and lipids in the control of breeding and on a range of hormonal and behavioural outcomes (e.g., Pravosudov et al. 2001, Schoech and Bowman 2003, Schoech et al. 2004). The findings of such studies have important implications for a wide range of management practices as well as understanding the complex nature of diet in the lives of animals (e.g., Arizmedi et al. 2007).

It is appropriate, therefore, to view the practice of wild bird feeding as a large-scale supplementary feeding experiment. Such experiments, however, are designed to test predictions about the role of food in the reproductive biology of focal species. For the millions of daily feeding 'experiments' being conducted world-wide, however, the aims appear to be primarily concerned with promoting observation and survival of birds. Furthermore, it is away from the feeders that the results of these experiments will be manifested, in the survival and breeding performance of supplemented birds. For almost all of the species using supplementary food sources, however, the long-term implications for

individuals, populations and communities are almost entirely unknown. Indeed, despite the ubiquity of garden bird feeding, remarkably little is known about the influences of supplementation on the population ecology of the birds involved. We contend that supplementary feeding of wild birds provides a wealth of research opportunities addressing how anthropogenic augmentation of food availability might influence birds. Here, we describe some important issues concerning the supplementary feeding of birds that remain poorly understood and suggest that it is time to explore them in more detail.

Why do we feed wild birds?

The obvious popularity of wild bird feeding would appear to be related to the pleasure it brings the participants, through intimate contact with wild animals, the exercise of humane concern, and the experiential knowledge gained from these encounters (Rohde and Kendle 1994, Miller 2005). These dimensions of bird feeding, although universally and intuitively asserted (Cannon 2000, Marshall 2004), nonetheless remain as assumptions until assessed more widely. For example, Howard and Jones (2004) conducted a study in Brisbane, Australia, where people engaged in feeding wild birds were asked to express their reasons for doing so. While a clear majority stated that the practice gave them pleasure, confirming what is intuitively apparent, a significant proportion of the participants also expressed their motivation in terms that the researchers termed 'environmental atonement': these people stated that they fed wild birds from a desire to redress human environmental impacts. For example, respondents stated "I want to try and undo some of the destruction caused by humans" and "We have destroyed their habitats, I want to give something back" (Howard and Jones 2004). These are strong sentiments and suggest a far more complex array of environmental and philosophical perceptions than may be expected from such a seemingly simple activity (Miller 2005).

Certainly participants in wildlife feeding feel strongly towards it and many endorse the frequently expressed opinion that wildlife feeding is of definite benefit to the animals involved (Howard and Jones 2004); the suggestion that feeding may be primarily for human enjoyment tends to be vigorously countered (Erickson 2003, Fitzpatrick 2003). Contemporary advocates of feeding typically highlight the broader conservation importance of the practice (Cannon 1999, Toms 2003, Marshall 2004, Cannon et al. 2005). In the UK, especially, domestic gardens are now the primary habitat supporting high proportions of national populations of numerous songbird species, including some that are declining such as the song thrush *Turdus philomelos*, with garden feeders almost certainly being a crucial resource (Cannon et al. 2005, Chamberlain et al. 2005). It is now commonplace to find the provision of supplementary foods by householders stated clearly as a fundamental means for facilitating wild bird survival in urban areas, in both popular articles (e.g., British Trust for Ornithology

2003, Toms 2003, Marshall 2004) and scientific research papers (e.g., Chamberlain et al. 2005, Schoech et al. In press).

While there are numerous concerns about the possible impacts of wild bird feeding (see below), many of which are openly acknowledged and discussed, there is also a growing debate over whether potential benefits adequately outweigh the likely impacts (Green and Higginbottom 2000). That feeding is regarded as a positive activity by many significant stakeholders and commentators within the feeding community is evidenced by the significant support forthcoming when the practice is questioned. The reaction from a large number of North American participants and organizations to a negative front-page story in *The Wall Street Journal* (Sterba 2002) and related articles (e.g., Rogers 2002) was marked and provided a valuable insight into the perceptions of both proponents and opponents (see Erickson 2003, Fitzgerald 2003). Nonetheless, despite the profuse and often detailed refutations of the many claims made in such reports, the reality is that extremely little factual information is currently available on which to establish constructive debate. This provides an obvious opportunity for productive collaborations between ornithologists and social scientists, and other specialists.

Concerns about the impacts of feeding

While feeding is likely to benefit the survival of individuals of certain species, it is also clear that the overwhelming majority of species fed in urban environments are abundant and widespread (Chace and Walsh 2006). Indeed, in the US and Australia, there are concerns that feeding may enhance populations of some introduced species, such as common starlings *Sturnus vulgaris* and house sparrows *Passer domesticus,* as well as certain larger and more behaviourally dominant species at the expense of native species (Chace and Walsh 2006, Parsons et al. 2006). In the UK, for example, recent increases in the number and distribution of feral rose-ringed parakeets *Psittacula krameri*, which out-compete most other garden bird species at feeders, is of concern (Cannon 2000). This is also a key concern in Australia, where the predominance of large and aggressive species such as pied currawongs *Strepera graculina* at feeding stations has been implicated in the local decline of numerous smaller and more subordinate species (Parsons et al. 2006). Corvids are a particular concern in the UK where apparent increases in urban-dwelling Eurasian magpies *Pica pica*, for example, have caused alarm among the feeding public (Cannon 1999). The presence of corvids in urban areas is often assumed to increase nest predation, although there is relatively little direct evidence of this (Marzluff and Neatherlin 2006). Nonetheless, in such cases, feeding may be indirectly responsible for declines in local avian biodiversity (Parsons et al. 2006).

Understanding the influence that wild bird feeding may be having on local biodiversity is only one of a number of reasons why investigating the implications of feeding is important. Additional concerns include the: possibility that fed birds may become

dependent on human-provided foods; spread of diseases; impact of inappropriate or nutritionally inferior foods on avian health and survival; loss of foraging skills; changes in movements and migration patterns; increases in interspecific and human-directed aggression. Although such concerns are widely discussed (Orams 2002, The Wildlife Society 2007), developing a sound basis for the promotion of best practice guidelines requires reference to a sound base of studies conducted on a broad diversity of species over a large spatial distribution.

The issue of dependence – the possibility that animals may become significantly reliant upon anthropogenic foods – is probably the most often cited concern regarding supplementation (Brittingham and Temple 1988, Sterba 2002). Until recently, the sole study to investigate this issue specifically found no evidence of dependency among winter-fed black-capped chickadees *Poecile atricapillus*, in Wisconsin, USA (Brittingham and Temple 1992). Interestingly, almost 80% of the diet of the fed birds was natural food items, despite easy-access to feeders. In studies of chick provisioning among blue tits *Cyanistes caeruleus* in the UK (Cowie and Hinsley 1988) and Florida scrub-jays *Aphelocoma coerulescens* in the US (Fleisher et al. 2003), only about 30% of the food brought to nestlings was not natural in origin.

In Australia, the diet of suburban Australian magpies *Gymnorhina tibicen* - the most common bird species using feeders throughout the country (Jones 2002) - was dominated by naturally-sourced soil and ground invertebrates obtained through natural foraging behaviours (O'Leary and Jones 2006). Moreover, most of the foods (86% of all items) brought to nestlings by breeding magpies were ground invertebrates, even though numerous feeding stations were readily available. This was an unexpected finding, especially late in the breeding cycle when pairs were often raising several chicks; despite the seemingly obvious energetic saving represented by diced sausage and ground beef, these magpies persisted with their demanding 'no-junk-food' policy in chick provisioning (O'Leary and Jones 2006).

While Australian magpies were clearly not dependent or even reliant on supplementary food, urban-dwelling Florida scrub-jays have been shown to consume significantly more human-provided foods than non-urban conspecifics (Sauter et al. 2006). Nonetheless, to date, there appear to have been no studies demonstrating dependency in any free-ranging species. There are, however, instances in which specific animals have become reliant on supplementary foods, although these were all in situations involving feeding wildlife for tourist benefits (Orams 2002) or to facilitate breeding in endangered species (Powesland and Lloyd 1994).

When freely-available supplementary foods are exploited by urban-dwelling species, there are several readily predictable outcomes, among the most consistent being a significant advance of breeding dates (Martin 1987, Boal and Mannan 1999). Studies of Florida scrub-

jays (Fleisher et al. 2003), certainly the best studied 'urban' species from the perspective of the influence of feeding, and Australian magpies (Rollinson and Jones 2002), have both shown that in some years populations with access to supplementary food can start breeding up to 17 and 13 days earlier, respectively, than unsupplemented conspecifics. Comparisons between urban and non-urban populations also reveal increases in the number of breeding attempts, greatly improved survival and often, but not always, improved reproductive output per year (Boal and Mannan 1999, Bowman and Woolfenden 2001, Rollinson and Jones 2002). In almost all such studies, the influence of bird feeders was strongly implicated.

While there is no doubt that the quality of many commercial seed mixes has steadily improved over recent years, many now providing nutritionally complete diets, concerns about the impact of unbalanced, inappropriate or inadequate food supplements remain prominent (Schoech et al. 2004). For example, numerous studies of feeding practice have shown that bread is one of the most common supplements provided world-wide (Orams 2002, Rollinson et al. 2003, Chace and Walsh 2006); whether the influence of this highly refined and processed food type on birds is useful, harmful or insignificant remains unknown despite its ubiquity.

There has been, however, an increase in interest in more specific nutritional aspects of wild bird feeding, although such studies are few in number (Pravosudov et al. 2001, Schoech and Bowman 2003, Schoech et al. 2004). For example, there is some evidence that Australian magpies that consume regular amounts of processed, high-lipid foods (e.g. meats - Rollinson et al. 2003) have elevated plasma cholesterol levels, although the long-term implications of this are not yet known (Ishigame et al. 2006). Certainly, some species appear to adjust their activity schedules in response to the nutritional nature of the food types available to them: Florida scrub-jays, for example, with access to a high fat-high protein supplement spent 12% less time foraging than wildland (unsupplemented) birds (Schoech et al. 2004). Nonetheless, surprisingly little is known about the nutritional and bio-physiological influences of the food types that are provided for wild birds, even though almost all such foods form no part of most species' natural diets. Well-publicised concern (e.g. see www.birdfeeding.com) over the apparent over-reliance - and possible resultant health issues - of some species on certain food types is an example of apparent self-regulation within the bird seed industry although dependable data on the extent of the use of these food types are, again, hard to obtain.

Feeders have been implicated in the spread of several important avian diseases (Bradley and Altizer 2006). Accessibility to a concentrated food source at a feeder inevitably results in an aggregation of birds where contact with infected individuals is much more likely (Brittingham and Temple 1988). In Australia, outbreaks of Psittacine Beak and Feather Disease and the spread of the bacterium *Clostridia* (which is associated with necrotising

enteritis) among lorikeets *Trichoglosus* spp. has been attributed to their frequent use of feeders (New South Wales NPWS 2003), although the link has yet to be established. In the UK, *Garden BirdWatch* (see http://www.bto.org/gbw/index.htm for details) participants are currently monitoring the incidence of Trichomoniasis following an outbreak of this disease among European greenfinches *Carduelis chloris* (Toms 2006). Similarly, data from large numbers of *Project FeederWatch* (see http://www.birds.cornell.edu/pfw/ for details) volunteers in North America (Dhondt et al. 2001) have provided the basis for a detailed understanding of the disease dynamics of the current epidemic of Mycoplasmal conjunctivis among house finches *Carpodacus mexicanus* (Dhondt et al. 2005).

The potential role of feeders in increasing disease risk is well recognised: almost all the material promoting and explaining feeding of wild birds includes prominent attention to hygiene (e.g., RSPB 2007); advice to *Project FeederWatch* participants, for example, has been especially explicit on this issue (Cornell Laboratory for Ornithology 2007). That the practice of feeding per se could be responsible for disease spread is, however, vigorously denied by supporters, who often cite a lack of direct evidence as support (Erickson 2003). In some cases, however, circumstantial evidence has been sufficient for the instigation of anti-feeding directives. For example, in an unusual reaction to disease outbreak, the Department of Fish and Game in California recently requested that feeders be temporarily removed from northern areas of the state in an attempt to limit the spread of a parasitic Trichomoniasis among band-tailed pigeons *Patagioenas fasciata* and mourning doves *Zenaida macroura* (Department of Fish and Game, California 2005). Whether such advice was followed remains unknown.

Promoting and opposing feeding

For some wildlife agencies and individuals, the apparent risks associated with the feeding of birds have led to well publicised attempts to control or ban the practice entirely. This is certainly the case in Australia where several state wildlife and conservation agencies strongly discourage all forms of wildlife feeding (Seipen and Stanley 1996, Tasmanian Parks and Wildlife Service 2002, Petrie et al. 2003). While these recent official reactions relate mainly to activities in reserves (Orams 2002), there are clear signs that some agencies would like to impose significant controls on wildlife feeding even in suburban and urban areas (Howard and Jones 2004). Despite the popularity of the practice in Australia (Rollinson et al. 2003), most agency publications that address the topic are invariably negative, typically listing the numerous concerns mentioned above, and suggesting strongly that feeding is harmful (Hunter 2001, Petrie et al. 2003).

In contrast, prominent Northern Hemisphere organizations such as the British Trust for Ornithology, Royal Society for the Protection of Birds, Cornell Laboratory of Ornithology

and many others actively promote wildlife feeding as an activity promoting conservation. Nonetheless, while these groups implicitly assume that feeding is beneficial to the birds as well as enjoyable to the human participants, there is also acknowledgement of many of the issues of concern. One prominent assertion is that feeding leads to closer contact with nature, which in turn enhances a 'conservation ethic'; people who feed birds are more likely to care more about conservation (Green and Higginbottom 2000). Interestingly, studies of support for conservation among bird watchers has yielded mixed results with some finding strong conservation interest and motivation while for others this was less certain (McFarlane 1994, Hvenegaard 2002).

It is evident that virtually all of the concerns and claims made by both proponents and opponents of the practice of providing supplementary food supplies - whether it is dependency, disease or dietary deficiency, or any of the numerous other important associated issues - research-based findings remain relatively rare. What is known with high levels of certainty, due to the amount of effort invested by the wild bird food industry itself, relates mainly to the preferences of the main target species: seed types, feeder design and, location, time of the day and season, food colour, taste and nutritional composition favoured or avoided (Dunn and Tessaglia-Hymes 1990, Kress 1998). These are crucial factors required to maximise bird visitation and consumption rates, and are constantly being assessed and monitored by a large and competitive global industry. However, with the focus on sustained study of such minutiae, the broader ecological and behavioural implications for species have been neglected to date.

Conclusion

What is certain, due to decades of careful supplementary feeding experiments conducted on a wide variety of taxa, is that alterations in the availability and quality of food resources can influence breeding activity. Whether these changes are important and positive or detrimental, however, cannot currently be discussed with clarity and certainty. Despite this, there can be little doubt that the feeding of wild birds is of profound importance to urban populations of birds. Moreover, it is an almost universal practice that is likely to increase in popularity; steadily urbanising Westerners, more and more divorced from contact with nature, appear to be searching for simple and meaningful ways of interacting with wildlife (Miller 2005). Feeding wild birds appears to be an obvious and effective means of doing so. Many people who enjoy feeding birds, and many of those who oppose the practice, are deeply concerned about its impacts.

Undertaking research in this context is not without significant logistical, ethical and methodological challenges. Almost unavoidably, studies of bird feeding in suburban landscapes have to cope with and account for the levels of community attention and

involvement often unfamiliar to many researchers. But carefully managed alliances between residents and researchers may provide opportunities normally unavailable for most of the latter. The truly phenomenal coverage of such 'citizen science' programmes such as *Project FeederWatch* in the US (Dhondt et al. 2001), *Garden BirdWatch* in the UK (Cannon et al. 2005) and the recently launched *Birds in Backyards* program in Australia, provide unprecedented details of the birds visiting suburban gardens. However, the success of such programs requires careful and critical attention to a range of methodological concerns.

Smaller-scale intensive studies, focussing on specific issues, are also essential, although it is likely that these will also require the cultivation of productive relationships with residents. Among the main priorities for investigation are issues of dependency, over-reliance on inappropriate supplements (including high oil-content seeds and protein-rich meats), and the implications for survival and reproduction of the individuals involved. Moreover, it is critical that we determine the percentage of overall diet constituted by supplementary foods for a range of species and during different seasons. Underlying this research aim is the requirement for research examining dietary shifts (and concomitant changes in foraging behaviour) between breeding and non-breeding stages of the annual cycle of focal taxa. Technological advances, such as stable isotope analysis and PIT tags, allow us to quantify the assimilation of food supplements (e.g., Davis et al. 2005) and visitation rates to feeders and broods (e.g., Freitag et al. 2001), respectively, providing invaluable insight into how food supplementation influences the nutritional ecology, breeding biology, health and, ultimately, the life history of birds feeding in urban environments.

We strongly encourage researchers, especially those already working in urban environments, to consider explicitly the role and influence of wild bird feeding on the avian populations that share our towns and cities.

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