



Bird ringing as a tool for behavioural studies

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Birds are an ideal model system for studying many aspects of animal behaviour. Throughout the last 100 years, ringing has been an essential tool in avian behavioural research as it allows birds to be identified and observed on an individual basis. Here, I introduce some of the most important and active research areas, including the study of dispersal, feeding behaviour, mating systems, sociality and vocal communication. This review highlights the pivotal role that ringing will continue to play in developing our knowledge and understanding of animal behaviour and the importance of an organised ringing scheme combining the efforts of volunteer ringers and scientists.

Over the last 100 years, the British Trust for Ornithology's Ringing Scheme has been hugely successful in establishing migration patterns and monitoring population dynamics for much of our avifauna (Wernham *et al* 2002, Balmer *et al* 2008). However, throughout this period, the Scheme and its counterparts around the world have also provided the infrastructure for a vast range of pure and applied scientific research, and behavioural studies in particular have benefited enormously from the development of organised ringing. In addition to being intrinsically interesting, the study of animal behaviour provides important insights into ecology, evolution and conservation, and it remains a thriving field (Alcock 2009). Birds have proven to be an ideal model system, and avian studies have played an instrumental role in developing our understanding of nearly all aspects of animal behaviour. Behavioural research invariably relies on the ability to identify animals on an individual basis and, throughout the last century, ringing has therefore provided an invaluable tool for making the scientific study of bird behaviour possible.

Ringing studies usually depend on at least some birds being recaptured or found dead. In behavioural research, it is often necessary to observe individuals on repeated occasions, or continually throughout their lives. For most species it is rarely possible to read ring numbers in the field and colour ringing has, therefore, become a widely used technique, allowing individuals to be identified and monitored in the field over relatively long distances and time periods. Moreover, the ease with which colour-ringed individuals can be resighted makes it possible for ringers, scientists and even members of the public to combine their observations and maximise the value of projects. One striking example is a long-term study of Black-tailed Godwits *Limosa limosa*, which combined the work of researchers with multiple resightings made by a large network of volunteers, enabling individual godwits to be tracked over successive

years as they travelled between Icelandic breeding grounds and wintering quarters in the UK and further south, and at all stopover sites along the way (Gunnarsson *et al* 2004). A complete review of the countless behavioural studies based on observations of ringed birds is beyond the scope of this paper. Instead, I briefly outline some of the most active and exciting areas of research into avian behaviour, highlighting the crucial part that ringing has played and will continue to play in each of them.

DISPERSAL BEHAVIOUR

Dispersal is one of the most important behavioural processes in ecology and evolutionary biology, and its role in driving demographic change also makes it a key focus for conservation (Clobert *et al* 2001). However, despite a huge empirical and theoretical literature, our understanding of dispersal behaviour remains surprisingly poor. Natal dispersal, the movement of an individual from its birthplace to the site where it first reproduces, is a major determinant of population dynamics and structure, but there are few good descriptions of natal dispersal patterns in birds and little is known about the factors underlying variation within and between species (Paradis *et al* 1998, Walters 2000). This is largely due to the biases inherent in most studies imposed by the finite size of study areas; the probability of detecting dispersal decreases with distance, and it is often impossible to distinguish dispersal from mortality (Koenig *et al* 1996, Nathan 2001). Despite these problems, however, bird ringing, and of course the ringing of pulli in particular, continues to shed light on natal dispersal behaviour. Some researchers have minimised bias to some extent by ringing on a huge spatial scale (Winkler *et al* 2005); others have combined colour ringing with mathematical bias corrections (Sharp *et al* 2008). Several recent studies have investigated dispersal direction as well as distance

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(Garant *et al* 2005, Matthysen *et al* 2005, Sharp *et al* 2008), a fundamental but usually overlooked component of natal dispersal patterns; these studies show that, in some species, siblings disperse in similar directions and that non-random patterns of dispersal can have a massive impact on population structure at a local scale.

Clear ecological, social and genetic influences on dispersal behaviour have been identified, both within and across species (Paradis *et al* 1998, Dingemanse *et al* 2003, Hansson *et al* 2003, Pasinelli *et al* 2004). Inbreeding avoidance is usually thought to be one of the main factors driving natal dispersal, but much of the evidence for this is based on theory; a long-term study of Great Tits *Parus major* recently provided some of the first empirical support, showing that birds known to have bred with a relative had dispersed far shorter distances than outbred individuals (Szulkin & Sheldon 2008). In addition to the ecological and evolutionary implications of dispersal, understanding the causes and consequences of this behaviour, and in particular the impact of dispersal patterns on the genetic structure of populations, is vital for conservation programmes (Macdonald & Johnson 2001, Dale *et al* 2005, Temple *et al* 2006). The use of ringing in conjunction with genetic procedures and modern tracking devices offers the most promising route for future research.

FEEDING BEHAVIOUR

All animals must eat to stay alive, and the study of avian feeding behaviour, facilitated by marking birds individually, has yielded many fascinating insights into the ways in which animals meet their energetic demands and the decision-making processes involved. Classic studies of Starlings *Sturnus vulgaris* (Kacelnik 1984), Oystercatchers *Haematopus ostralegus* (Meire & Eryvynck 1986) and Northwestern Crows *Corvus caurinus* (Zach 1979) showed how individuals are able to optimise their foraging strategy according to the spatial distribution and abundance of their food, its energy content, and the time it takes to find and process particular food types. More recently, researchers studying Knots *Calidris canutus* have found that individuals can also adjust their feeding behaviour in relation to the digestion time of particular prey items (van Gils *et al* 2005), and can integrate prior knowledge about feeding sites with their foraging success to maximise energy intake rate (van Gils *et al* 2003). Many species forage socially, and individuals in flocks often adopt different behavioural tactics for obtaining food. Traditionally, these tactics have been broadly classified as either 'producing' (*ie* searching for food independently) or 'scrounging' (*ie* joining others who have found food). Ringing studies have shown that individuals vary whether they produce or scrounge according to predation risk (Barta

et al 2004), dominance (Wiley 1991), condition (Lendvai *et al* 2004), experience (Katsnelson *et al* 2008) and the kinship of flock members (Toth *et al* 2009). Kinship has also been found to influence the trade-off between foraging efficiency and predation risk in flocks of Siberian Jays *Perisoreus infaustus* (Nystrand 2007).

Some birds, and in particular the corvids, show extraordinary cognitive abilities in their feeding behaviour (Emery & Clayton 2004). The New Caledonian Crow *Corvus moneduloides* is one of very few species that manufactures and uses tools for acquiring otherwise unobtainable food, and it does so with a proficiency more usually associated with primates (Hunt 1996, Weir *et al* 2002). Tool use in these birds has mostly been investigated in captivity, but a recent colour-ringing study has allowed researchers to explore the cognitive processes behind this remarkable behaviour in a wild population (Holzhaider *et al* 2008). Research on food hoarding or caching behaviour has also been highly productive in the study of animal cognition. Clark's Nutcrackers *Nucifraga columbiana*, for example, can store many thousands of pine seeds and recover them several months later, whereas Western Scrub-jays *Aphelocoma californica* cache a smaller number but wider variety of food items and recover them over shorter periods relative to how perishable they are (Emery & Clayton 2004). Individuals that cache food are also able to modify this behaviour according to the risk posed by both heterospecific and conspecific thieves, and even adopt counter-strategies such as storing food behind visual barriers or caching inedible items (Dally *et al* 2006). Again, many researchers have used captive corvids as model systems, but a number of field studies involving other taxa have provided fresh insights. Brotons (2000), for example, showed that in a wild colour-ringed population of Coal Tits *Periparus ater* individuals frequently hoard food in winter but are less likely to do so in the presence of close neighbours, challenging the idea that caching in the Paridae is restricted to species that defend their resources in territories outside the breeding season.

MATING SYSTEMS AND PARENTAL CARE

The remarkable diversity of animal mating systems has always been a core subject in behavioural research. Until relatively recently, monogamy was thought to be the most common system in birds and Lack (1968) famously concluded that over 90% of passerines were monogamous. However, this idea has been completely turned on its head with the development of molecular tools and their application in avian research. In reality, true genetic monogamy is known to occur in only 14% of passerines; in most socially monogamous species, males

and females regularly seek extra-pair copulations (Griffith *et al* 2002). Avian mating systems in fact range from strict monogamy through various forms of polygamy to complex polygynandrous systems in which multiple mating by both sexes is common. Understanding this variation remains an active research area and one that, perhaps better than any other, illustrates the value of combining behavioural observations of ringed birds with genetic methods.

The widespread occurrence of extra-pair paternity in socially monogamous species has led to the development of several hypotheses concerning the benefits to females. These include guarding against male infertility, maximising genetic compatibility with partners and increasing the genetic diversity or quality of offspring (Griffith *et al* 2002, Akcay & Roughgarden 2007). Studies of Great Tits, Blue Tits *Cyanistes caeruleus* and House Sparrows *Passer domesticus* have provided evidence of fertility insurance (Wetton & Parkin 1991, Krokene *et al* 1998), but support for the various hypotheses of genetic benefits is mixed. Recent work has shown that females may gain such benefits in Reed Buntings *Emberiza schoeniclus* (Bouwman *et al* 2006) and Bluethroats *Luscinia svecica* (Fosroy *et al* 2008), but not in Blue Tits (Charmantier *et al* 2004), for example, and comparative analyses suggest that overall support for these hypotheses is weak (Akcay & Roughgarden 2007). Furthermore, several authors have concluded that extra-pair paternity may not be female driven at all (Westneat & Stewart 2003, Eliassen & Kokko 2008). Understanding the function of this behaviour and explaining interspecific variation remain important challenges.

Mating-system evolution is closely related to variation in forms of parental care and the roles of the sexes. Biparental care is the most common pattern in birds, but the relative contribution of males and females is highly variable within and between species (Cockburn 2006). In some species, parents have been shown to provision their young at consistent rates within and across years (Nakagawa *et al* 2007), and feeding rates can even be partly heritable (MacColl & Hatchwell 2003). However, parental investment is often far less predictable and, as it incurs future reproductive and survival costs, males and females are in conflict over how hard to work (Clutton-Brock 1991). In sexually promiscuous Dunnocks *Prunella modularis* and Reed Buntings, males provision offspring in relation to the proportion they are likely to have sired (Burke *et al* 1989, Dixon *et al* 1994). Recent studies of other species, including House Sparrows (Schwagmeyer *et al* 2002, Nakagawa *et al* 2007) and Great Tits (Sanz *et al* 2000, Hinde 2006), have explored how individuals respond to the work rate of their partners, revealing a complex negotiation process.

In interspecific brood parasites there is no parental care at all, perhaps the most familiar example being the Cuckoo *Cuculus canorus*. In this species, the single chick manipulates

the provisioning rate of its host parents by producing begging calls that mimic the sound of a whole brood (Davies *et al* 1998, Kilner *et al* 1999). Females specialise in parasitising a single host species, and recent work has shown that in one 'host-race', begging-call types are not genetically fixed but chicks appear to learn by experience which to use (Madden & Davies 2006). However, the anti-predatory pause in begging in response to the species-specific alarm calls of host parents seems to be largely innate (Davies *et al* 2006).

SOCIAL BEHAVIOUR

Despite the highly competitive nature of reproduction and survival, many animals spend at least part of their lives in groups. The study of sociality has been a dominant component of behavioural research throughout its history, not least because of the implications for understanding our own species, and avian systems have proven to be enlightening. Among the most frequently suggested benefits of group living are reduced predation risk and increased foraging success. The chances of being eaten may simply be diluted in larger groups, which might also confuse predators; the probability of detecting a predator may be increased, and by spending less time being vigilant individuals can spend more time feeding. Many studies of birds have shown that vigilance is indeed lower in larger flocks (Beauchamp 2008), but several reviews have suggested that, overall, the relationship between group size and vigilance is unclear (Lima 1995, Roberts 1996). Furthermore, work on Redshanks *Tringa totanus* has shown that reduced vigilance does not lead to increased feeding rates because in larger groups there is greater interference competition (Sansom *et al* 2008). However, evidence for the dilution effect and predator confusion has been found in the same species (Cresswell 1994), and a review of social foraging in birds concluded that feeding in groups is often associated with an increased intake rate (Beauchamp 1998).

In some species, individuals don't simply form groups but live socially and interact cooperatively. Apparently-altruistic behaviour in animal societies presents something of an evolutionary paradox, as acting for the benefit of others at the expense of oneself seems to challenge the central tenets of natural selection. The most influential idea for explaining altruism, and understanding social behaviour more generally, was provided by kin selection theory (Hamilton 1964, Maynard Smith 1964): individuals can pass on their genes to future generations indirectly by increasing the reproductive success of relatives. Cooperative breeding systems, in which so-called helpers forego reproduction and, instead, assist others rear their offspring,

are ideal models for testing this theory, and bird studies have again been pivotal. Around 9% of all bird species are thought to breed cooperatively (Cockburn 2006), and one of the few European examples is the Long-tailed Tit *Aegithalos caudatus*. A long-term study of this species in which all adults and pulli in the population are colour ringed each year has allowed researchers to monitor the life histories of individuals of known relatedness, and demonstrate the importance of kin selection in social evolution. Towards the end of the breeding season, many failed breeders become helpers rather than attempting to re-nest, and experiments have shown that helpers preferentially allocate their care to close kin (Russell & Hatchwell 2001), whom they recognise from family-specific calls they learn as nestlings (Sharp *et al* 2005). Helpers increase the productivity of the broods they attend (Hatchwell *et al* 2004), and nest failure is so common in this species that many individuals gain reproductive success only indirectly via helping (MacColl & Hatchwell 2004).

VOCAL COMMUNICATION

The study of bird song has been at the forefront of research on animal communication for decades, but has also been invaluable in enriching our understanding of many other aspects of behaviour (Slater 2003, Catchpole & Slater 2008); ringing has again been essential. Bird song is widely accepted to have the two major functions of mate attraction and territorial defence (Catchpole & Slater 2008), and some species even appear to have different songs for different purposes (Nelson & Croner 1991, Spector 1991, but see Beebee 2004). A classic study of Great Tits (Krebs 1977) remains one of the best examples of how singing repels rivals, but the precise role of song in mate choice is still being explored. In some species, such as the Sedge Warbler *Acrocephalus schoenobaenus*, females are more attracted to males with larger repertoires (Buchanan & Catchpole 1997), but a recent review concluded that such preferences are not as widespread as once thought (Byers & Kroodsma 2009). Similarly, reviews of vocal mimicry suggest that this phenomenon results from imperfect song learning rather than repertoire acquisition and may be relatively unimportant for female choice (Garamszegi *et al* 2007, Kelley *et al* 2008). However, song structure can provide females with information about male quality. Evidence from Sedge Warblers (Buchanan *et al* 1999) and Great Tits (Bischoff *et al* 2009), for example, indicates that song may signal parasite load or exposure to parasites in early life, and Blackcap *Sylvia atricapilla* song rates have been shown to correlate negatively with parental care, but may indicate territory quality (Hoi-Leitner *et al* 1993).

Although most research on vocal communication in birds has focused on song, bird calls have also been a highly productive subject. The begging calls of nestlings, for example, have provided an ideal model for investigating communication and conflict between parents and offspring (Kilner & Johnstone 1997, Horn & Leonard 2008), and alarm calling is a key component of anti-predatory behaviour (Griesser 2008). The coordination of many behavioural interactions depends on individuals or groups being able to recognise each other, and bird calls have been shown to facilitate recognition between mates (Robertson 1996, Mulard *et al* 2008), parents and their offspring (Lefevre *et al* 1998, Mulard *et al* 2008), siblings (Nakagawa & Waas 2004), and kin more generally (Sharp *et al* 2005). Calls were traditionally considered to be genetically determined (Marler 2004) and, despite a long history of research on song development (Slater 2003), investigations of call acquisition were scarce. More recently, however, several calls have been found to be learnt (Hughes *et al* 1998, Sharp *et al* 2005, Keenan & Benkman 2008), and ongoing research into behavioural learning and development will benefit from the study of both calls and song (Marler 2004).

CONCLUSIONS

This brief overview of some of the major research areas in behavioural studies underlines the fundamental part that bird ringing continues to play in developing our knowledge and understanding of animal behaviour. The ability to identify and monitor birds on an individual basis underpins most behavioural research, and the development of new technology, such as satellite trackers, and methodology, for example genetic techniques and stable-isotope analysis, has complemented rather than replaced ringing. Although this kind of work generally falls outside the main aims of most ringing schemes, these schemes offer an excellent basis for research into avian behaviour. Furthermore, direct collaboration between volunteer ringers and professional ornithologists can be highly rewarding for both parties, and will hopefully become increasingly common in the future as communication technology makes such exchanges ever easier.

Finally, much of the research discussed here would simply not be possible without sound ringing practice and techniques. Safe handling with minimal impact on the birds is imperative for both ethical and scientific reasons; after all, there is little point in marking individuals for behavioural study if the process of marking itself influences their behaviour. Ageing and sexing methods are also important research tools, and the accurate

recording of biometrics is an essential process in many studies. It is therefore vital that the very best training and ringing procedures are maintained and continually refined. Relatively few British ringers are professional ornithologists, but over the last 100 years the work of volunteer ringers in providing training and collecting data has laid the foundations for a great deal of exciting and important research into animal behaviour.

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