CHAPTER 1

Incubating new ideas about avian reproduction

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1.1 Scientific study of eggs and nests

One of our earliest engagements with the natural world, and more specifically with ‘wild animals’, is as children when many of us have discovered a nest full of eggs (and often a vociferous bird defending it against all intruders). It is small wonder that we are fascinated by nests that in some cases can be marvels of architecture and construction, while in others they encapsulate functional simplicity. Contained within nests are eggs that have long captivated our attention with their marked variation across species in number, size, shape, and colour. For some the mesmerism of nests and eggs endures into adulthood as evidenced by the success of the Nest Record Scheme (NRS) of the British Trust for Ornithology (BTO). Every spring and summer some 500 volunteer nest recorders (amateur and professional ornithologists alike) visit approximately 30,000 nests of many different species (Greenwood 2012; Chapter 17). In addition there are some museum collections (detailed for Europe by Roselaar 2003) that hold exceptionally large collections of nests and eggs. For example, the Natural History Museum in Tring (NHM Tring), UK contains approximately 4,000 nests and some 400,000 sets of eggs (Russell et al. 2013).

Despite deep-rooted interest from field ornithologists, nests and eggs have received relatively little attention as the main focus of study and it is only comparatively recently that they have come to the fore (Figure 1.1; Colllias and Colllias 1984; Hansell 2000; Deeming 2002a; Ferguson-Lees et al. 2011). We suspect that the dramatic increase from the 1990s to the present day in the number of these publications does not reflect a sea change in interest in nests and eggs per se. Rather, it results from a wholesale increase in the number of technologies now available to the field biologist, in the number of outlets, i.e. journals, for such published work, in our abilities to collate information about such publications, and in interest in general ornithology ‘across the board’. The latter point was acknowledged by Birkhead et al. (2014) who stated, ‘In 2011 there were as many papers on birds published as there had been during the entire period between Darwin’s Origin [Darwin 1859] and 1955.’ Although we are not writing a history of ornithology as part of this introductory chapter, as an important historical reference point it is worth noting that according to Haffer (2007) so-called ‘New Avian Biology’, i.e. the transformation of the discipline of ornithology from natural history into a modern [and mainstream] biological discipline, was attributable to one man. He was Erwin Stresemann (1889–1972) who was the Curator of Ornithology at the Museum of Natural History in Berlin, Germany. Haffer (2007) argued that Stresemann was responsible for transforming ornithology into the modern biological discipline we recognize today, because he sought to unite systematic and field ornithologists by pursuing answers to functional questions related to the morphology, physiology, and behaviour of birds.

Despite this ‘new dawn’ for modern ornithology, as described by Haffer (2007), we contend that the study of nests and eggs has not received the degree of support from professional ornithology that it warrants. Based upon our contention, it is tempting to predict that the number of published studies about the nest and egg stages of avian life history has lagged behind those addressing other traits. However, when we examined the published literature since 1990, i.e. the threshold decade for escalation of published outputs about nesting biology (Figure 1.1), a key word search in Web of Science using life-history traits (sensu Bennett and Owens 2002) revealed no apparent ‘lag’ in the relative numbers of published papers addressing reproductive events of birds at the nest versus those outside of it (Figure 1.2). It
is striking that only papers reporting development and breeding (as a general term) exceeded in number those reporting on nesting biology. Furthermore, the number of papers documenting studies of incubation, laying, and hatching ‘held their own’ against those describing fledging and recruitment (Figure 1.2). Nesting biology is a broad topic and knowledge of the construction of nests as functional (reproductive) units is relatively poor but slowly improving (Chapters 3 and 4).

1.2 A reluctance to engage?

Our contention does not relate to the number of published outputs about nests and eggs. Rather, we argue that ornithologists have been reluctant to engage fully with the study of nesting birds and we attribute this to a number of reasons. The first of these is related to concerns that any activity undertaken by researchers in the vicinity of a nest could influence the data that

Figure 1.1 The results of a search of the Web of Science database using ‘nest*’ AND ‘bird*’ OR ‘egg*’ AND ‘bird*’ as key words to determine the number of papers published per decade during the 20th and 21st Centuries. Note that 5,375 papers were published between 2010 and 2013 (inclusive) and a further 571 papers have already been published in 2014.

Figure 1.2 The results of a search of the Web of Science database using ‘bird*’ AND various life-history traits as key words to determine the number of papers published per year between 1990 and 2013 (inclusive). Key words used (with focal life-history trait[s]): Recr.—‘recruit*’ (recruitment); Fled.—‘fledg*’ (fledging); Incub.—‘incubat*’ (incubation); Hatc.—‘hatch*’ (hatching); Lay.—‘lay*’ (laying); Surv.—‘surviv*’ (survival); Grow.—‘grow*’ (growth); Nest.—‘nest*’ (nest-building, nesting and nestling); Deve.—‘develop*’ (development); and Breed.—‘breed*’ (breeding). Note that a literature search of papers published in 2014 was not performed as we were only midway through the year at the time of writing.
are generated—this is the basis of the ‘uncertainty principle’ of Heisenberg (1927) who predicted that the very process of collecting data could exert influence on the nature of the results. Ornithologists have long recognized that this principle could be applied particularly to studies at the nest and they have rightly adapted their nest monitoring protocols to minimize disturbance. Once a nest is discovered and marked appropriately (Ferguson-Lees et al. 2011), ornithologists remain worried that their activities increase its susceptibility to loss from predation by mammals and by both heterospecific (Quinn et al. 2008) and even conspecific birds (e.g. Garvin et al. 2002), and from brood parasitism (Davies 2000). While in some cases such concerns are well-founded (e.g. Anderson and Keith 1980; Pierce and Simons 1986), in others findings are equivocal.

Until recently, the direct effects of our activities at the nest have not been quantified; instead, researchers have ‘erred on the side of caution’ in their experimental approach. However, Ibáñez-Álamo et al. (2012) carried out a meta-analysis on results from 18 published nest predation studies and found that the activities of researchers did not increase subsequent nest predation. In some orders, such as the Passeriformes, they even found evidence for a positive relationship between human activity at the nest and nest survival (see further discussion in Reynolds and Schoech 2012). Despite these latest findings, we should remain vigilant in designing and executing our nest monitoring protocols to minimize predation risk to adults, eggs, and chicks alike.

Perhaps some of the caution in assessing the ‘observer effect’ at the nest (Reynolds and Schoech 2012) lies in our inability to identify what to measure. Possible observer effects might range from nest abandonment (resulting in exposure and starvation of nestlings) to subtle changes in nest attendance by adults that result in alterations to the physiological state and nutritional condition of nestlings. For example, Rensel et al. (2010) found that nestling stress levels, as determined from measures of the avian stress hormone corticosterone, were positively correlated with the proportion of time that female breeding Florida scrub-jays (Aphelocoma coerulescens) (Figure 1.3) spent away from the nest. Developmental conditions, especially as they relate to exposure to corticosterone, may have profound and chronic effects upon a bird’s physiological and behavioural phenotype (Schoech et al. 2012). Note that throughout this book we follow Gill and Wright (2006) in our use of scientific and common nomenclature of avian taxa.

Such considerations of the adverse consequences of nest disturbance are timely as they coincide with those related to other ornithological activities, such as mist-netting (Spotswood et al. 2012) and blood sampling (Arnold et al. 2008; Brown and Brown 2009). Meticulous planning of future studies, and reflection on past studies, promote the adoption of experimental approaches that are effective in acquiring robust data while also promoting the welfare and long-term survival of birds. Indeed, many researchers already seek permissions from national authorities before ringing breeding birds and chicks, and visiting nests, while local and national ethical reviews take place before licenced procedures (e.g. tissue sampling) can be carried out at the nest. For those who are research-active at nests in the UK, approaches must be justified within the context of the so-called 3Rs, i.e. Replacement, Refinement, and Reduction (Festing et al. 2002). The legislative path in the UK can be somewhat hampered by the rather ambiguous definitions of what constitutes ‘a procedure’ and thus what requires a Home Office licence, particularly when dealing with embryos (Deeming 2011a). There is no doubt that considerable legislation associated with research at the nest has partly engendered a reluctance to engage, especially within the ranks of amateur ornithologists (see Foreword). We refer the reader to Toms (2011) for further details related to such matters.

1.3 A renewed interest in nests and eggs?

Over the 20th Century there was considerable interest in avian incubation, driven particularly by a need to improve artificial methods for hatching large numbers of poultry eggs. Understanding of the avian egg and embryonic development was greatly enhanced by studies during the 1930s through to the 1960s (see Romanoff and Romanoff 1949, 1972; Romanoff 1960, 1967), particularly for the domestic fowl (Gallus gallus). In the late 1960s through to the 1980s the work of Rahn, Paganelli, Ar, and numerous colleagues (Rahn and Paganelli 1981; Seymour 1984; Whittow and Rahn 1984; Rahn et al. 1985; Metalfe et al. 1987; Deeming and Ferguson 1991a; Tullett 1991) developed a more detailed knowledge of embryonic physiology and egg biology in a wider range of bird species, often in natural nests. One consequence of these extensive studies was perhaps a general view that we had ‘cracked’ the key elements of avian incubation biology. Whilst interest in nests and incubation behaviour was prolonged and sustained over the century, there was considerable
emphasis on the ecology of nesting but few scientific syntheses of how birds reproduced (Drent 1975) until reviews by Hansell (2000) and Deeming (2002a). Since that time interest in incubation has extended to reptiles (Deeming 2004a) and there has been an increasing use of technology in the study of nesting (Ribic et al. 2012). Use of novel analytical techniques that allow investigation of phylogenetic effects on biological patterns have also been applied to eggs (Deeming et al. 2006; Deeming and Birchard 2008; Deeming 2007a, 2007b, 2008; Birchard and Deeming 2009; Birchard et al. 2013; see Chapters 9 and 11).

Despite ongoing considerations about how we measure the impacts of research activities at the nest, researchers are beginning to appreciate that the nesting biology of birds may considerably shape our understanding of how birds invest time and energy during their breeding attempts. Such considerations may markedly change how we view life-history strategies across species (e.g. Martin and Li 1992) and decision-making during breeding attempts within species (e.g. de Neve and Soler 2002). Both perspectives partly explain the intensity of behaviours such as incubation effort (including nest attentiveness), nest defence, brood provisioning, and even nest construction by adult birds.

Since the publication of Deeming (2002a), there has been a sustained output of published papers reporting on the nesting biology of birds (Figure 1.2). While we are not suggesting that this is a causative relationship, there may be a number of contributing factors that underlie this trend. For example, so-called ‘Citizen Science’ (Greenwood 2007; Dickinson and Bonney 2012) has gained momentum with the growing popularity of various established volunteer schemes at both the BTO (e.g. NRS) and the Cornell Lab of Ornithology (e.g. NestWatch) resulting in the public engaging much more in the study of breeding birds (Chapter 17). The harnessing of the power of citizen science to generate data over long temporal and large spatial scales will undoubtedly result in closer associations between ornithological agencies. It is noteworthy that a formal agreement was signed between the BTO (e.g. NRS) and the Cornell Lab of Ornithology (e.g. NestWatch) resulting in the public engaging much more in the study of breeding birds (Chapter 17). The harnessing of the power of citizen science to generate data over long temporal and large spatial scales will undoubtedly result in closer associations between ornithological agencies. It is noteworthy that a formal agreement was signed between the BTO and Cornell in 2013 signalling closer collaboration than ever before (see various chapters in Dickinson and Bonney 2012; Chapter 17). We hope that this also signals continued closer associations between amateur and professional ornithologists in this regard.

Arguably, since the publication of Deeming (2002a), rapid advances in the technologies used in video cameras (MacDonald and Bolton 2008) and thermocouples (de Heij et al. 2007), have allowed remote nest monitoring to take place at relatively modest expense to researchers while imposing relatively little disturbance on adult birds in attendance. This has resulted from miniaturization that has made devices much less obvious at the nest and from increased efficiency of
batteries reducing frequency of nest visits by researchers to replace them. Technologies are now widely available through commercial suppliers and practical and theoretical information about their effective deployment is available through the scientific literature (e.g. Ribic et al. 2012; Chapter 15) and often from the larger commercial suppliers themselves.

For some of the world’s most threatened species, a need for more detailed knowledge about their nesting biology has been clearly identified for their effective conservation (Chapter 16). For example, in the critically endangered kakapo (Strigops habroptilus) a programme of supplementary feeding allowed researchers to determine that low breeding frequency was due to nutritional constraint (Elliott et al. 2001). In California condors (Gymnogyps californianus) effective breeding to fuel a reintroduction programme was only achieved because of detailed knowledge about the microclimate under which eggs taken from the wild were artificially incubated (Kuehler and Witman 1988). The fundamental importance of food availability to breeding performance of Florida scrub-jays was only revealed through prolonged study of birds at the nest (Figure 1.3). Schoech et al. (2008) clearly demonstrated the potency of food supplementation as a tool to increase both clutch size and chick survival. Increasingly, our understanding of food (Robb et al. 2008) and the key role that it plays in breeding performance is arming conservation biologists in their efforts to translocate populations and to restore native habitats.

1.4 Unexplored gaps in our knowledge

There remain some unexploited areas of ornithology which would certainly be fruitful for future research investigating nests and eggs. For example, we have already acknowledged the nest and egg collections of the NHM Tring, UK (see Section 1.1), but the Western Foundation of Vertebrate Zoology (WFVZ) in Camarillo, CA, USA contains over 18,000 nests and some 225,000 sets of eggs. Although such UK and US collections make major and valuable contributions to scientific research activities, much more use of such collections could be made by researchers (Collar et al. 2003). As an example Russell et al. (2013) asked 140 staff at 112 museums in 37 European countries about the use of their nest collections and discovered that of the only 8% of staff that responded, most reported limited internal and external use of collections for research purposes over the previous decade. Russell et al. (2013) acknowledged that this can be explained partly as a failure in outreach to communicate widely the contents of museum collections. However, the under-use of such collections can also be explained by limited accessibility to them (but see Russell et al. 2010), and many museums have taken major steps recently to address this issue by starting to database their entire nest collections. It is essential that the gap between workers in the field and museum curators is bridged to ensure that collections are fully exploited for research purposes. It should be noted, however, that museums are generally reluctant to allow researchers to use their materials in a manner that leads to their destruction. Although excess materials can be supplied for research (e.g. Portugal et al. 2014a) and whilst it is an understandable perspective to prevent damage, this can rather restrict the level of engagement between museum collections and researchers.

Fjeldså (2013) suggested that in our research efforts to discover new species, there should be continued collecting of materials to augment museum collections. He described museums as having lost their appetite for collecting in the mid-20th Century when ornithologists, overburdened by regulations governing collecting, turned their attentions to studies of ecology and behaviour of birds in the field. He rightly argued that museum collections still provide much of the data upon which conservation status and descriptions of species in modern field guides are founded. However, interestingly, Fjeldså (2013) provided ‘some elements’ of a useful description of a new species but they lack any reference to nest or egg traits as being useful descriptions for specimens. For comprehensive discussions about the fundamental role that museums play in research, we refer the reader to Collar et al. (2003).

We are concerned that even the basic breeding biology is not known for some species. For example, while the reproductive strategies of brood parasites such as the common cuckoo (Cuculus canorus) have been studied for centuries (Jenner 1788; Darwin 1859; Davies and Brooke 1988; Portugal et al. 2014b), the finer details of how chicks of one well-known genus of brood parasites, the honeyguides (Indicator spp.), kill host chicks were only revealed in the last few years (Spottiswoode and Koo revaar 2012). Furthermore, many ornithologists investigate how ecological parameters influence clutch size (e.g. Lack 1947; Ricklefs 1980; Slagsvold 1982), but for many species nest descriptions remain poor despite eggs having been counted within them! In perhaps the most comprehensive study of clutch size to date, Jetz et al. (2008) gathered data on clutch sizes of 5,290 bird species, excluding those of brood parasites and pelagic species. In their analyses they included ‘nest type’ as an explanatory variable but they only included nest data for 2,816 species (or 53.2% of species for which they had
clutch size data). Of course, the authors only had access to sources of primary data that had been published prior to their analyses. For example, for *Handbook of the Birds of the World*, information about nest type was only available for species described up to and including volume 11 (del Hoyo et al. 2006). It is estimated that now nest descriptions could be extended to approximately 4,500 species (W. Jetz, personal communication) of the 9,993 species described in Jetz et al. (2012). However, it is clear that a major shortfall in nest descriptions for many species exists.

Finally, the emerging new field of ethno-ornithology (Tidemann and Gosler 2010) may promise much in furthering knowledge of nests and eggs. It attempts to use traditional ecological knowledge (e.g. information within folklore, nursery rhymes, stories) to augment scientific ecological knowledge about species, thereby expanding our ornithological knowledge (e.g. Sinclair et al. 2010). We envisage that as sources of information contributing to traditional ecological knowledge, such as the Ethno-ornithology World Archive (EWA 2014), expand, so too will our knowledge of the nesting biology of birds, both past and present.

1.5 The structure of ‘Nests, Eggs, and Incubation’

This book builds upon the strong foundations laid down by Deeming (2002a). However, *Nests, eggs, and incubation* is not simply a postscript to it because it is over 12 years since *Avian incubation: behaviour, environment, and evolution* was conceived, written, and published. Understanding of egg biology, nest function, and incubation behaviour has improved in the interim and, of course, during our early discussions there was a strong justification (see Preface) for an updated version of Deeming (2002a). However, some topics in the original book remain valid and relevant and effectively up to date because there has been little substantial progress in further understanding. By contrast, new knowledge has been accrued in many different fields not necessarily covered in the original volume. Therefore, rather than revising Deeming (2002a), we have extended the review of avian egg biology and incubation so as to complement the original, which is now available for readers of this book as a free online resource (see the Preface for more details). The structure of this book is illustrated in Figure 1.4 in which

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**Figure 1.4** A schematic diagram illustrating the overall structure of the book. At its centre is the breeding cycle of a typical avian species with key life stages shown in boxes, biological processes linking stages shown in italicized text and the numbers of relevant chapters referring to each stage and/or process shown in dark grey boxes.
we have shown the avian breeding cycle, its constituent life stages, the biological processes that link sequential stages, and the relevant numbers of chapter(s) of the book that refer to each stage/process. It is clear that the book covers most of the avian breeding cycle except the fledgling stage, which is defined as the period between a young bird fledging and becoming fully independent of its parents (Cox 1996). Among avian life historians ‘fledging’ is a rather poorly defined unsatisfactory event which has been intensely debated in the literature (e.g. Middleton and Prigoda 2001) and in many species fledging is so transient that little is known about it.

After starting with an updated consideration of the evolution of avian reproductive biology, the book is divided into four broad areas: the nest, the egg, incubation, and the study of avian reproduction. Our understanding of the role of nests has improved greatly since Deeming (2002a) and so these structures are given greater consideration in this book. Other chapters update our understanding of the egg traits and life history as well as incubation as a process, including the currencies of investment paid by breeding birds. We also consider how modern methodologies as diverse as self-contained temperature probes and citizen science help us to gain greater insights into nests and eggs as functional units. The last section of the book includes chapters describing how such basic biological knowledge can be applied to challenges such as defining, and responding to, conservation issues and climate change. We conclude by attempting to define areas that are priorities for future research addressing these key stages of the avian breeding cycle.

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