

From Bullfinches to Cuckoos: Sperm, eggs and embryos – some ornithological mysteries solved

Tim Robert Birkhead

From Bullfinches to Cuckoos: Sperm, eggs and embryos – some ornithological mysteries solved. – The idea of the ‘the scientific method’ implies that research usually proceeds in a logical, step by step fashion, but in reality, the process is often messier. Using my own research as an example I describe how a succession of serendipitous and apparently unrelated events resulted in the resolution of a long-standing ornithological mystery: internal incubation. An interest in the cultural history of bird keeping and a throw-away comment by a bird breeder resulted in a study which revealed the extremely unusual reproductive biology of the Eurasian Bullfinch. In an attempt to understand why interspecific hybridisation with the male Bullfinch is never (or very rarely) successful we developed a method to distinguish between infertile eggs, early embryo mortality and parthenogenesis in unhatched eggs. These techniques allowed us to investigate and verify the existence of ‘internal incubation’ in certain brood parasitic birds, including the European Cuckoo. Retention of fully formed eggs in the oviduct for an additional 24 hours, during which time embryo development continues, results in the egg of the European Cuckoo hatching about 30 hours ahead of host eggs laid at the same time.

Keywords: Bullfinch *Pyrrhula*, Canary *Serinus*, Cuckoo *Cuculus canorus*.

Tim R. B i r k h e a d , Department of Animal & Plant Sciences, The University of Sheffield, Sheffield S10 2TN, UK, E-Mail:T.R.Birkhead@sheffield.ac.uk

The course of true love and scientific research rarely run smoothly or directly. There’s a naive belief that research typically proceeds in an orderly progression of logical steps as a result of the ‘scientific method’. Sometimes it does, but often the process is messier, although few researchers seem to be prepared to admit to that. The problem is exacerbated

by the editors of scientific journals more or less demanding that research is written up as though it had taken place in a clear, logical, step-by-step manner – even if it hasn't! Here I offer an illustration of the serendipitous nature of research, using some of my own recent work as an example.

Throughout my career the main focus of my research has been a topic known as “post-copulatory sexual selection” - the causes and consequences of female promiscuity. Post-copulatory sexual selection comprises sperm competition (the competition between the sperm of different males to fertilise the eggs of a particular female) and cryptic female choice (the ability of females to differentially utilise the sperm of the different males they have mated with) (DAVIES et al. 2011). Most of my scientific research has focussed on birds, but I am also interested in the history of science, and as a consequence the history of ornithological science. Precisely because the history of ornithology began with the study of birds in captivity, I have been fascinated by the cultural history of bird-keeping. For many people, including many ornithologists the idea of bird-keeping is unacceptable, and indeed in many countries it is now largely illegal. As a consequence, the information acquired by bird-keepers both past and present, and hence much of the history of ornithology, has been overlooked (BIRKHEAD 2008).

This story starts in 2000 when I was collecting material for *The Red Canary* – an account of the way bird-breeders in the 1920s transformed ordinary yellow canaries into a red bird by crossing with the Red Siskin *Carduelis cucullata* (BIRKHEAD 2003). To get some idea of how bird-keepers operated, I started to give talks at bird-keeper's clubs. The first of these, in Doncaster, northern England, was somewhat daunting for both parties since neither of knew what to expect (BIRKHEAD 2003:6-7). The evening started out badly but ended up well, and after my talk, in which I had mentioned the cloacal protuberance of male finches, one of the audience came up to me to tell me that the male Bullfinch *Pyrrhula pyrrhula* lacked a cloacal protuberance. I was intrigued because in an earlier study we had found that the relative size of the cloacal protuberance in different species was a good indicator of both the numbers of stored sperm and the intensity of post copulatory sexual selection. Species with a large protuberance were typically rather promiscuous, so the fact that the male Bullfinch has no protuberance suggested that it might be highly monogamous.

My informant told me he had a dead Bullfinch in his fridge at home that I could dissect to see just how many sperm it had. One thing led to another and over the next year or so I was able to examine the cloacal protuberance, testes and sperm of several Bullfinches. Not only did they have tiny testes (in fact their testes are among the smallest relative to body size of any species), they also had the most unusually designed sperm of any bird I had seen (Fig. 1). The Bullfinch's sperm are completely unlike those of any other finch, and indeed of any of the 250 passerine species that my research students and I have examined (BIRKHEAD et al. 2006, 2007; DURRANT et al. 2010). I concluded that because of a lack of sperm competition (deduced from the tiny testes), selection had favoured Bullfinches that produce the most basic kind of sperm – enabling them to direct their energies into other structures or activities. As long as the sperm fertilised the female

Bullfinch's eggs, they were adequate. To illustrate this I can use an analogy with a car journey. If you had to drive from Munich to Bremen and it didn't matter when you arrived, any kind of car would suffice, even an old Trabant. If, on the other hand it was a race and you were competing with others, then a Porsche would be best. By analogy, in species like the Dunnock *Prunella modularis*, where sperm competition is intense, each of their sperm is like a Porsche – beautifully designed; the Bullfinch – with no competition - has Trabant sperm.

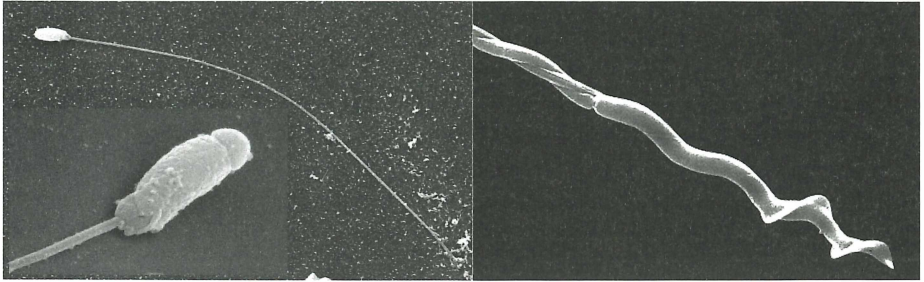


Fig. 1. Bullfinch spermatozoa (left two images; upper: the entire sperm, total length 49 μm ; lower: the head showing the rounded acrosome and lack of mitochondrial helix on the flagellum) compared with that of a typical passerine sperm of a House Sparrow *Passer domesticus*.

My interest in bird-keeping goes back to my teenage years when I kept variety of finches and was fascinated by the fact that it was possible cross different finch species to produce gorgeous hybrids. I also remembered reading that the male Bullfinch was almost the only finch species that would *not* hybridise with other another finch or the domestic canary (also a finch). When bird-keeping was at its peak in the nineteenth and early twentieth-centuries there must have been many thousands of attempts to cross the male Bullfinch and female canary – citizen science of a kind – with the very clear result that the male Bullfinch is incapable of producing hybrid offspring. The female Bullfinch does hybridise with other finches, albeit with difficulty (BIRKHEAD & VAN BALEN 2007).

I wondered whether the male Bullfinch's unique sperm might account for its inability to hybridise: perhaps its unusual sperm simply couldn't reach or fertilise the egg of another species.

I decided to try to test this hypothesis. And so began one of the most tedious experiments I have ever conducted. Over several years I obtained a total of 36 male Bullfinches and 36 female canaries and paired them together. I knew I would never get hybrid offspring but I wanted to see whether the Bullfinch sperm could function inside the canary female reproductive tract. I did this by examining the layer of tissue (the so-called

perivitelline layer) that surrounds the yolk. If I found Bullfinch sperm on the perivitelline layer of the Canary eggs resulting from these mixed pairings this would mean that the sperm had successfully traversed the entire oviduct, providing clear evidence that the sperm design was not a problem.

Over four years my students and I examined 379 eggs from 99 clutches – hardly a trivial effort since apart from maintaining the birds in my garage, each perivitelline layer took a minimum of one hour to examine under the microscope. In the vast majority of cases there were no sperm on the eggs. This was what I expected since getting a Bullfinch and a Canary to form a pair bond is difficult, getting them to copulate is even more difficult: the female canary is fickle, but once she's decided to solicit for copulation she's impatient. The male Bullfinch by contrast, is like an old man and takes his time, such that the female canary had usually lost interest by the time he was ready to copulate. However, in 10 cases, we did find sperm on the perivitelline layers of eggs, showing clearly that in some pairs at least copulation had occurred and that the Bullfinch's unusual sperm had successfully traversed the female reproductive tract.

In none of those ten eggs was there any obvious sign of embryo development. This suggests that fertilisation had not taken place. However, I knew from the poultry literature that even though an egg might have been fertilised, the embryo could die at a very early stage, often just a few hours after fertilisation, making it very hard to distinguish between a lack of fertilisation and early embryo death.

Even though it was obvious that in some instances the Bullfinch sperm could reach the Canary egg, I had no way of knowing whether the Canary eggs had been fertilised or not. The poultry literature contains papers from the 1940s describing how by examination of the germinal disc one can decide whether a Chicken *Gallus domesticus* or Turkey egg *Meleagris gallopavo* has been fertilised, but the method seemed rather imprecise and probably not appropriate for a small bird like a Canary. I was anxious to know at what stage the Bullfinch sperm failed: before or immediately after fertilisation? Bird-keepers, unable to distinguish between the two, usually refer to such eggs as 'clear', meaning that the egg shows no signs of development and usually assume that the egg has not been fertilised, but as our later research showed true infertility (insufficient or no sperm) is rare (BIRKHEAD et al. 2008a).

Since I was unable to reach any firm conclusion about the performance of Bullfinch sperm in the Canary oviduct, I was also unable to convince my favourite ornithological journal that the results were worth publishing. Concerned that the little knowledge I had gained during those tiresome experiments did not go to waste, I published the results in a bird-keepers' newspaper (BIRKHEAD et al. 2008b). A scientific failure? Perhaps. On the other hand, it was a failure that led – eventually – to a success, albeit in a completely different area. My failure prompted me to develop an incontrovertible method for distinguishing between eggs that had not been fertilised and eggs that had been fertilised but the embryo died, often at a very early stage.

The eggs of most birds like Canaries and Chickens are fertilised about 24 hours before the egg is laid. The ovum (the yolk - which bears the germinal disc containing the

female genetic material) is released from the ovary into the top of the reproductive tract early in the morning and fertilisation takes place within a few minutes. The ovum then moves down the reproductive tract having the white (albumen) and shell put on, and the fully formed egg is laid about 24 hours later. In other words, fertilisation occurs some 24 hours before the egg is laid. In several species of domestic poultry, and probably in passerines as well, the embryo starts to develop about six hours after fertilisation, so that by the time the egg is laid, the germinal disc contains thousands of cells (which are visible only under the microscope).

Working with various students, I devised a method that allowed us to look at unhatched eggs and to decide whether they had, either not been fertilised or had been fertilised and the embryo had died. An undergraduate student Nicola Hemmings, working under my supervision, conducted most of the work to develop this method, building on a previous study of House Sparrows *Passer domesticus* eggs (BIRKHEAD et al. 1995). As well as using captive Zebra Finches *Taeniopygia guttata*, she also examined the unhatched eggs of wild Tree Sparrows *Passer montanus* and showed that even in eggs that are several weeks old and well and truly addled (and very smelly), it is still possible to establish exactly why the egg has failed to develop (BIRKHEAD et al. 2008a).

Armed with this new methodology – which took several years to perfect - it would now be possible to repeat the male Bullfinch x female Canary experiment and establish when the Bullfinch sperm fail: before or after fertilisation, but so far, I haven't done it.

The other thing our study of unhatched eggs revealed was the existence of parthenogenetic development in passerine birds. Parthenogenesis is the development of a diploid embryo from an unfertilised egg, that is, with no contribution from the male, (also known as virgin birth). Common in certain invertebrate taxa, parthenogenesis occurs more rarely in vertebrates, notably in fish and reptiles, and is extremely rare in birds. Prior to our study parthenogenesis had been recorded only in only four bird species, and most famously in domesticated Turkeys (OLSEN 1965). A visiting MSc student to my laboratory, Elske SCHUT, noticed that in eggs laid by female Zebra Finches that had not been with a male for several months, there were in some cases large numbers of cells in the germinal disc indicating that parthenogenetic development had occurred (SCHUT et al. 2007). Essentially these were randomly organised sheets of cells which eventually died. Exactly the same situation had been found in domesticated Turkeys in the 1950s. In that case however, intense artificial selection and some careful husbandry over five years finally resulted in the production of parthenogenetic offspring (OLSEN 1965). I like to think that with several years of artificial selection, we too could produce a strain of parthenogenetic Zebra Finches.

At around the time we had completed our work on unhatched eggs, I was discussing the history of the study of brood parasitism in the Common Cuckoo *Cuculus canorus* with Karl Schulze-Hagen and Bård Stokke (see SCHULZE-HAGEN et al. 2009). It was during these discussions that we realised it might be possible to use the techniques we had developed to distinguish fertile and infertile eggs, to test the little-known and somewhat mysterious notion of 'internal incubation' in the Cuckoo.

In his landmark volume *Ecological Adaptations for Breeding in Birds*, David LACK (1968: 87-88) comments on the short incubation periods in cuckoos and the fact that they usually hatch before the host young: ‘while the embryo develops rapidly in the egg, the incubation period is further shortened in a least two cuckoos, *Clamator jacobinus* (LIVERSIDGE 1961) and *Cuculus canorus* [Common Cuckoo], because they retain the egg in the body unusually long, so that it is incubated prior to laying *for about eighteen hours longer than in normal birds*’ [my italics – see below]. LACK continues: “I have known for many years that this was said of *C.canorus*, but have failed to find a reference; it is confirmed by a single recent record by C. M. Perrins, *pers. comm.*.” [see PERRINS (1967)].

Interestingly, the fact that the embryos of recently laid cuckoo eggs are advanced compared with those of their host species had been noticed by egg collectors before LIVERSIDGE (1961) or PERRINS (1967), for example, by NETHERSOLE-THOMPSON (1951) and CLAUDON (1955). However, because ‘oology’ has for many years been, like bird-keeping, a ‘forbidden area’ of ornithology, these observations were ignored or over-looked. Desmond NETHERSOLE-THOMPSON who was a well-respected if controversial ornithologist commented in his book *Greenshanks* (1951: 150) that ‘I have strong evidence that greenshanks (and incidentally hobbies, cuckoos and certain other birds as well) are able to retain their eggs for limited periods if they are disturbed during egg-laying’. Nethersole-Thompson could only have deduced this from an examination of the embryo of eggs collected soon after laying.

The reference that Lack failed to find and the origin of the idea of internal incubation, was George Montagu’s *Ornithological Dictionary*. In the Introduction to his Dictionary, MONTAGU (1802: xv) says this: ‘The consequence of this retention would be a dilation of the embryo by the internal heat of the body, and the foetus advanced towards perfection in proportion to the time the egg remained in that state’.

How did Montagu reach this remarkable insight about egg retention and internal incubation in the Cuckoo? First, he was aware of the concept of internal incubation since he refers to its occurrence in the snake, the Viper *Vipera berus*, which hatches its young by the internal heat of its body’ (MONTAGU 1802: xv). Second, he either knew or inferred that Cuckoos differed from most other birds by laying at intervals of greater than 24 hours. It seems unlikely that he had direct evidence for a 48 hour laying interval: this was apparently first discovered by REY (1892: 61-68), although credit is usually given to Edgar CHANCE (1922: see WYLLIE 1981; DAVIES 2000). Indeed, with respect to the laying interval CHANCE (1922: 31) states ‘the results of our own investigations will doubtless be regarded as proofs of the soundness of Rey’s reasoning’ (CHANCE 1922: 31). MONTAGU (1831) makes it clear that he knew that most birds lay at intervals of 24 hours, and appears to have deduced, on the basis of advanced embryo development (see below), that the female Cuckoo can retain its egg and as a consequence lays at intervals greater than 24 hours. His explanation for egg retention is that it provides the Cuckoo with longer to locate appropriate host nests (MONTAGU 1831: 119). Third, Montagu tells us that he dissected ‘many Cuckoos’ and recovered a fully formed eggs from the oviducts of several females (MONTAGU 1813 – under ‘Cuckow’ – pages

unnumbered; MONTAGU 1831: 119). It is likely that as an astute observer and egg collector used to emptying freshly laid eggs he recognised that embryo development in some Cuckoo eggs taken from the oviduct was further advanced than in other species. A comment about the fact that the Cuckoo's eggs are invariably larger than those of its hosts provides a clue to Montagu's conclusions. He says: 'If therefore, the embryo of the Cuckow [sic] was not sometimes enlarged before the egg was laid, is it reasonable to suppose it would be first hatched?' (MONTAGU 1802: xvi).

It is the word "sometimes" that provides the clue. By looking for signs of embryo development in fully formed eggs taken from the Cuckoo's oviduct, Montagu must sometimes have encountered eggs just 24 hours after fertilisation (and exhibiting no obvious sign of development), but he would also have found eggs that had been in the oviduct for longer, hence the fact that *sometimes* they showed a more advanced state of development. Montagu's insight - overlooked by most subsequent collectors of cuckoo eggs (see for example MAKATSCH 1937; BALDAMUS 1892; BAKER 1942) and most subsequent Cuckoo researchers - is remarkable. The only ornithologist who recognised and commented on Montagu's idea was E. M. NICHOLSON (1926).

We capitalised on the new techniques together with the fact that there are now many cuckoo researchers across Europe. Through their help we obtained eight freshly laid Cuckoo eggs and compared the stage of embryo development with a number of other species (Fig.2), confirming that all the cuckoo eggs were advanced compared with all other species that lay at 24 hour intervals (BIRKHEAD et al. 2009).

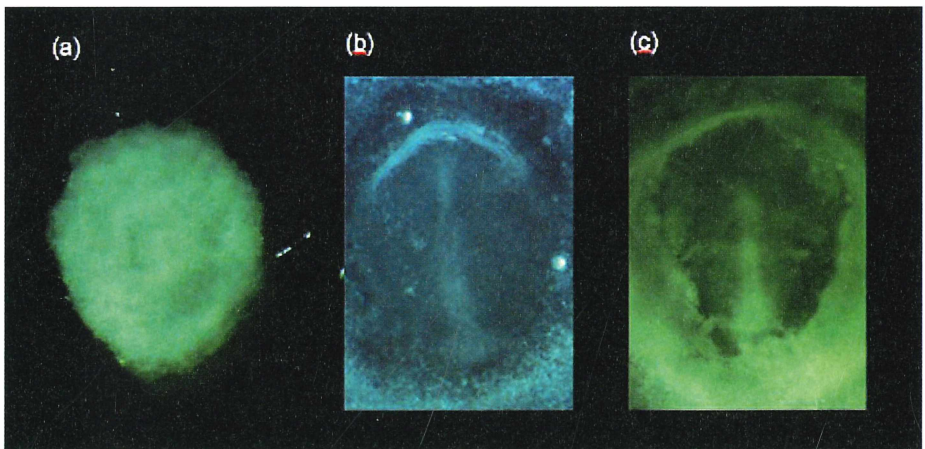


Fig. 2. Germinal disc of (a) a Zebra Finch at the time of laying, (b) a Zebra Finch after an additional 24 hours of incubation at body temperature (40°C) rather than normal incubation temperature (36°C); (c) Cuckoo at the time of laying. Note that the stage of embryo development in (b) and (c) are identical.

LIVERSIDGE (1961) suggested that 'at laying the development of the Jacobin Cuckoo is approximately 17-20 hours advanced on the normal chick embryo', and as we have seen (above) Lack assumed an 18-hour advantage in the Common Cuckoo. To test whether this was correct, we first took the eggs of the Zebra Finch immediately after laying and incubated them at (Cuckoo) body temperature (40°C) for an additional 24 hours, to mimic the egg being retained in the oviduct of the female Cuckoo. After 24 hours of incubation at 40°C the Zebra Finch embryos were at exactly the same stage of development as the Cuckoo embryo at laying. Second, we compared the number of additional hours of natural incubation a Zebra Finch embryo required to reach a similar stage of development as the Cuckoo at laying. This showed that at laying the Cuckoo embryo is about 30 hours ahead of other birds in its development. We assume that this comes about for the following reasons. The cuckoo embryo starts to develop some 5 or 6 hours after fertilisation (as in other birds), and because it is retained inside the female cuckoo's body for 24 hours longer than other birds it gains a 18 hour advantage. However, because the internal body temperature of the female cuckoo is about 40°C, some 4°C warmer than normal incubation temperature, the overall advance is about 30 hours (BIRKHEAD et al. 2009).

In conclusion, a chance remark by a bird-keeper led me to look at the reproductive system of the male Bullfinch, revealing several unique, but inter-related features. Indeed, that single observation initiated a research programme exploring the role of post-copulatory sexual selection in sperm design and eventually provided an explanation for the enormous diversity in sperm shape and size across the animal kingdom (IMMLER et al. 2011). My failure to identify whether Canary eggs had been fertilised by Bullfinch sperm, encouraged me to develop a method for distinguishing between genuinely infertile eggs and eggs that have been fertilised but whose embryo dies before there are any obvious signs of development. That technique has now been used to identify and resolve breeding problems in captive breeding programmes including that of the critically endangered Spix's Macaw *Cyanopsitta spixii* (HEMMINGS & BIRKHEAD, in preparation). Also, as described here, we have used that technique to resolve the issue of internal incubation in the Cuckoo. My aim in this account has been partly to demonstrate the course of scientific research does not always run true, but also to demonstrate the different types of input that can shape scientific research; in this case by citizen science, serendipitous comments by non-scientists and by an awareness of the history of particular disciplines.

Zusammenfassung

Von Gimpeln zu Kuckucken – Spermien, Eier, Embryonen und die Lösung eines Vogelrätsels. – Wissenschaftliches Arbeiten verläuft geradlinig und in einer Abfolge

von logischen Schritten. So jedenfalls die ideale Vorstellung. Von einem solchen Ideal ist die Realität allerdings weit entfernt; nur allzu oft erweist sie sich als kurvenreicher Hindernislauf. Meine eigenen Forschungsprojekte können durchaus als Beispiel dafür herhalten, wie glückliche Umstände und Fakten ohne ersichtlichen Zusammenhang auf einmal, in der richtigen Kombination, die Lösung eines Rätsels ergeben. In diesem Fall das Rätsel der internen Bebrütung bei Vögeln. Es war mein Interesse an der Kulturgeschichte der Vogelhaltung, das zur Einladung zu einem Vortrag vor Kanarienzüchtern führte. Als in der anschließenden Diskussion einer der Vogelhalter von den Schwierigkeiten bei der Zucht von Gimpeln in Gefangenschaft berichtete, war ein neues Thema auf dem Tisch; es ging um deren von den anderen Finken stark abweichende Reproduktionsbiologie. Weil es völlig rätselhaft war, warum Gimpelmännchen bei der Kreuzung mit anderen Finken praktisch nie Nachkommen erzeugen, entwickelten wir Techniken, mit denen an unfruchtbaren Eiern untersucht werden kann, ob es gar nicht zur Befruchtung gekommen ist, ob der Embryo früh abgestorben ist oder ob gar die ersten Entwicklungsstadien einer Parthenogenese vorgelegen haben (was gar nicht so unwahrscheinlich ist). Mit einer solchen Technik konnten wir dann an frischgelegten Eiern von mehreren Brutparasiten, darunter dem Kuckuck, nachweisen, dass in diesen Eiern die Embryonalentwicklung aufgrund einer „inneren Inkubation“ bereits eingesetzt hatte. Die Erklärung hierfür ist, dass bei einigen brutparasitierenden Vogelarten das fertige Ei nicht sofort gelegt, sondern für weitere 24 Stunden im Ovidukt verbleibt und dass der Embryo sich in dieser Zeit „im Mutterleib“ entwickelt. Auf diese Weise bekommt der junge Kuckuck einen Vorsprung von etwa 30 Stunden vor gleichzeitig gelegten Wirtseiern.

Acknowledgements

I am extremely grateful to Rolf Schlenker who, through his extensive knowledge and library, gave me a wonderful introduction to the fascinating and overlooked early literature on bird-keeping. Without him, I'd never had got started. Many others have assisted in the various research projects mentioned here, notably Nicola Hemmings. I owe special thanks to Karl Schulze-Hagen and Bård Stokke who as well as providing a great deal of stimulating conversation and ideas, made helpful comments on the manuscript. Finally, I thank all the bird-keepers who helped with our Bullfinch experiments by providing birds.

References

BAKER, E. C. S. (1942): Cuckoo Problems. London (Witherby). – BALDAMUS, E. (1892): Das Leben der europäischen Kuckucke. Berlin (Parey). – BIRKHEAD, T. R. (2003): The Red Canary. London (Weidenfeld & Nicolson). – BIRKHEAD, T. R. 2008: The Wisdom of Birds - an Illustrated

- History of Ornithology. London (Bloomsbury). – BIRKHEAD, T. R., S. IMMLER, E. J. PELLATT, & R. J. FRECKLETON (2006): Unusual sperm morphology in the Eurasian bullfinch *Pyrrhula pyrrhula*. Auk 123: 383-392. – BIRKHEAD, T. R., F. GIUSTI, S. IMMLER, & B. G. M. JAMIESON (2007): Ultrastructure of the unusual spermatozoon of the Eurasian bullfinch (*Pyrrhula pyrrhula*). Acta Zoologica 88: 119-128. – BIRKHEAD, T. R. & S. VAN BALEN (2007): Unidirectional hybridisation in birds: an historical review of bullfinch (*Pyrrhula pyrrhula*) hybrids. Archives Natural History 34: 20-29. – BIRKHEAD, T. R., J. HALL, E. SCHUT & N. HEMMINGS (2008a): Unhatched eggs: methods for discriminating between infertility and early embryo mortality. Ibis 150: 508-517. – BIRKHEAD, T. R., N. HEMMINGS, E. SCHUT, & S. FITZPATRICK (2008b): Why bullies miss the bullseye. Cage & Aviary Birds, June 5: 15. – BIRKHEAD, T. R., J. P. VEIGA, & F. FLETCHER (1995): Sperm competition and unhatched eggs in the house sparrow. J. Avian Biology 26: 343-345.
- CLAUDON, C. (1955): Nouvelles observations sur *Cuculus c. canorus*. Linné en Alsace. L'Oiseau 25: 44-49.
- DAVIES, N.B. (2000): Cuckoos, cowbirds and other cheats. London (Poyser). – DAVIES, N. B. (2011): Cuckoo adaptations: trickery and tuning. J. Zool. 284: 1-14. – DAVIES, N. B., H. R. KREBS, & S. WEST (2011): An Introduction to Behavioural Ecology. Oxford (Blackwell). – DURRANT, K. L., D. A. DAWSON, T. BURKE & T. R. BIRKHEAD (2010): The unusual sperm morphology of the Eurasian bullfinch (*Pyrrhula pyrrhula*) is not due to the phenotypic result of genetic reduction. Auk 127: 832-840.
- IMMLER, S., S. PITNICK, G.A. PARKER, K.L. DURRANT, S. LUPOLD, S. CALHIM & T.R. BIRKHEAD (2011): Resolving variation in the reproductive trade-off between sperm size and number. Proceedings National Academy of Sciences 109: 5325-5330.
- LACK, D. (1968): Ecological adaptations for breeding in birds. London (Methuen). – LIVERSIDGE, R. (1961): Pre-incubation development of *Clamator jacobinus*. Ibis 103: 624.
- MAKATSCH, W. (1955): Der Brutparasitismus in der Vogelwelt. Radebeul (Neumann). – MONTAGU, G. (1802): Ornithological Dictionary. London (White). – MONTAGU, G. (1813): Supplement to the Ornithological Dictionary. Exeter (Woolmer). – MONTAGU, G. (1831): Ornithological Dictionary of British Birds [edited by James Rennie]. London (Hurst, Chance & Co).
- NETHERSOLE-THOMPSON, D. (1951): Greenshanks. London (Collins). – NICHOLSON, E. M. (1926): Birds in England. London (Chapman & Hall).
- OLSEN, M. (1965): Twelve-year summary of selection for parthenogenesis in Beltsville small white turkeys. British Poultry Science 6: 1-6.
- REY, E. (1892): Altes und Neues aus dem Haushalte des Kuckucks. Leipzig (Freese).
- SCHULZE-HAGEN, K., B. STOKKE & T. R. BIRKHEAD (2009): Reproductive biology of the European cuckoo *Cuculus canorus*: early insights, persistent errors and the acquisition of knowledge. J. Orn. 150: 1-16. – SCHUT, E., N. HEMMINGS & T. R. BIRKHEAD (2007): Parthenogenesis in a passerine bird, the zebra finch *Taeniopygia guttata*. Ibis 150: 197-199.
- WYLLIE, I. (1981): The Cuckoo. London (Batsford).

ZOBODAT - www.zobodat.at

Zoologisch-Botanische Datenbank/Zoological-Botanical Database

Digitale Literatur/Digital Literature

Zeitschrift/Journal: [Ökologie der Vögel. Verhalten Konstitution Umwelt](#)

Jahr/Year: 2012

Band/Volume: [34](#)

Autor(en)/Author(s): Birkhead Tim

Artikel/Article: [From Bullfinches to Cuckoos: Sperm, eggs and embryos - some ornithological mysteries solved 547-556](#)