60 YEARS OF ANIMAL BEHAVIOUR

Anniversary Essay

The past, present and future of 'cuckoos versus reed warblers'

Mary Caswell Stoddard [a],[*], Rebecca M. Kilner [b]

[a] Harvard University, Department of Organismic and Evolutionary Biology and Museum of Comparative Zoology, Cambridge, MA, U.S.A.
[b] University of Cambridge, Department of Zoology, Cambridge, U.K.

ARTICLE INFO

With their landmark publication 'Cuckoos versus reed warblers: adaptations and counteradaptations' (Animal Behaviour, 1988, 36, 262–284), Davies & Brooke ushered in a new era of research on avian brood parasitism. Building on centuries of rich natural history and detailed observation of common cuckoos, Cuculus canorus, Davies & Brooke (1988) performed a set of simple but powerful experiments to understand the adaptive value of a female cuckoo's behaviour as she parasitizes a host nest. In this essay, we explore the historical backdrop against which Davies & Brooke began their field experiments in Wicken Fen. We then evaluate four conceptual innovations made by Davies & Brooke (1988) involving rejection costs, egg mimicry, frontline defences and chick discrimination, and we show how these advances have shaped research in the last 25 years. Davies & Brooke (1988) paved the way for diverse and dynamic research on avian brood parasites, and we conclude by highlighting several promising new directions for the future, namely the genomics of adaptation, sensory ecology and cognition.
© 2013 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

In the summers of 1985 and 1986, Nick Davies and Michael Brooke took to the English fens to conduct their now classic experiments on the coevolutionary interactions between the common cuckoo, Cuculus canorus, and one its favourite hosts, the reed warbler, Acrocephalus scirpaceus. Their results, published in 'Cuckoos versus reed warblers: adaptations and counteradaptations' (Animal Behaviour, 1988, 36, 262–284), helped introduce the study of brood parasitism to mainstream behavioural and evolutionary ecology. The paper is long ('excessively long', complained one of its referees) but much more than the sum of its many parts. It is so rich in natural history that we can almost smell the fens as we read it, yet it is packed with incisive interpretation of simple experiments addressing clear questions about the nature of adaptation. Through field observation, elegant experimentation and innovative synthesis, Davies & Brooke (1988) established a benchmark for behavioural analyses of coevolution and adaptation, laying the foundations for

future research in areas such as the genomics of adaptation and speciation, sensory ecology and cognition.

HISTORICAL BACKGROUND: NATURAL HISTORY AND COEVOLUTIONARY ARMS RACES

Like many good empiricists, Davies & Brooke (1988) begin with Aristotle. He was the first known writer on cuckoo biology and recorded in the fourth century BC that common cuckoos 'do not sit, nor hatch, nor bring up their young, but when the young bird is born it casts out of the nest those with whom it has so far lived' (Hett 1936, cited in Davies & Brooke 1988, page 262). These early observations suggest that the common cuckoo's parasitic habit has been known for millennia, although little formal study of cuckoo biology materialized before 1700 AD (Schulze-Hagen et al. 2009). Interest in the common cuckoo enjoyed a revival during the European Enlightenment, which promoted science and natural history. The keen observations of early ornithologists (reviewed in Schulze-Hagen et al. 2009) revealed critical insights into the common cuckoo's behaviour, including the fact that female cuckoos

* Correspondence: M. C. Stoddard, Harvard University, Department of Organismic and Evolutionary Biology and Museum of Comparative Zoology, 26 Oxford Street, Cambridge, MA 02138, U.S.A.
E-mail address: mstoddard@fas.harvard.edu (M. C. Stoddard).

Figure 1. Cuckoos versus reed warblers at the egg-laying stage. Common cuckoos, *Cuculus canorus*, have evolved egg mimicry in response to egg discrimination by reed warblers, *Acrocephalus scirpaceus*. Shown here is a reed warbler nest containing three host eggs and one cuckoo egg (lower right). Photo: N. Davies.

often lay mimetic eggs (Fig. 1), produce relatively small eggs, and deposit their eggs before the host has completed her clutch. With no theory of natural selection, however, these observations often generated somewhat rosy interpretations of the cuckoo's behaviour. Bechstein (1791, cited in Davies 2000, page 9), for example, described 'the great delight the birds show when they see a female Cuckoo approach their abode' and noted that host birds relish 'the honour which the great bird confers upon them by selecting their nest for its own use'. Darwin's (1859) theory of natural selection dismissed this kind of interpretation and showed how to evaluate the cuckoo's behaviour in terms of the parasite promoting its own self-interest. In *The Origin of Species*, Darwin devoted a paragraph to explaining how the cuckoo's parasitic behaviour might have evolved under natural selection, a contribution that cannot be undervalued. Davies (2000, page 8) commented that 'Darwin packs more good ideas into these four sentences than all previous commentators on the Cuckoo since Aristotle'.

Darwin's insights inspired a new generation of cuckoo naturalists, many of whom collected eggs and conducted egg exchange experiments to great effect. Baldamus (1892) and Rey (1892), for example, used their own egg collections to demonstrate that female cuckoos always lay the same type of egg, a fact confirmed by molecular techniques more than a century later (Moksnes et al. 2008). Alfred Newton, the first professor of Zoology in Davies and Brooke's own Department at Cambridge and also an avid egg collector, termed the word 'gens' to describe the different egg morphs (1896). The acquisition of detailed natural history on the common cuckoo reached its zenith from 1918 to 1925, when Edgar Chance spent long hours chronicling the behaviour of female cuckoos in Worcestershire, England. Meanwhile, biologists discovered that they could play the part of the cuckoo by placing eggs in the nests of potential hosts. It was this experimental technique (reviewed in Schulze-Hagen et al. 2009) that showed that hosts actively defended themselves against the activities of the cuckoo. These experiments, pioneered by Lottinger (1776) and Blyth (1835), were first used systematically by Swynnerton (1918), Baker (1923) and then Rensch (1925), who added foreign eggs to the clutches of different species to investigate the mechanisms and consequences of egg recognition.

The early researchers of cuckoo biology not only documented the natural history of the adaptations and counteradaptations later analysed by Davies & Brooke (1988): they too realized the evolutionary significance of these traits. Swynnerton (1918), for example,

suggested that host discrimination against odd-looking cuckoo eggs would result in the evolution of cuckoo egg mimicry (see also Baker 1923). The evolution of mimetic cuckoo eggs, in turn, would favour hosts that could somehow discriminate between their eggs and one laid by the cuckoo (Fig. 1). Interactions between cuckoos and hosts could therefore afford the opportunity to 'watch natural selection at work' (Swynnerton 1918).

Some years later, and following Williams's (1966) ground-breaking insights into the nature of adaptation, the pioneering work of Stephen Rothstein (1975) and Robert Payne (1977) described the behaviours shown by brood parasites and their hosts in terms of their adaptive value. Rothstein's (1975) and Payne's (1977) detailed and meticulous field studies helped bridge the divide between the natural historians who first studied brood parasite–host interactions and the behavioural ecologists analysing brood parasitism today. Building on the egg replacement experiments pioneered by Rensch (1925), Rothstein (1975) performed the first controlled, large-scale experimental study of brood parasitism, replicating natural cowbird parasitism by placing hundreds of artificial (and occasionally real) eggs in the nests of 43 potential host species. His synthesis revealed that host species can easily be defined as 'accepters' or 'rejecters', that the accepters and rejecters are not phylogenetically distinct, and that ejection by hosts typically occurs by egg removal rather than by egg burial or desertion. Both Rothstein and Payne showed how the interactions between brood parasites and their hosts ideally lend themselves to the scientific study of adaptation, ideas reinforced by Dawkins & Krebs (1979) and couched in terms of an asymmetric coevolutionary arms race. Dawkins & Krebs (1979) explained how adaptations for successful parasitism by common cuckoos could be countered by increasingly refined adaptations by hosts, which could in turn select for even better tricks on the part of the cuckoo. It was precisely these ideas that Davies & Brooke (1988) put to the test in the Cambridgeshire fens.

Interestingly, while Davies and Brooke were carrying out their experiments, three other teams were independently working in the field on the interactions between brood parasites and their hosts. In Norway, Arne Moksnes had been making detailed observations about the interactions of Norwegian hosts and the common cuckoo for more than 10 years. He and Eivin Røskaft then began conducting egg replacement experiments, inspired by Rothstein's work. They published their findings a few months later than Davies & Brooke (1988) in October 1988 (Moksnes & Røskaft 1988). In Australia, Michael and Lesley Brooker were studying all 11 endemic brood parasites but focused in particular on the interactions of Horsfield's bronze-cuckoos, *Chrysococcyx basalis,* and shining bronze-cuckoos, *Chrysococcyx lucidus*, with their hosts. The Brookers also used experiments with model eggs, publishing their work in 1989 (Brooker & Brooker 1989). And in Japan, Hiroshi Nakamura (1990) was using model egg experiments to test the hypothesis that common cuckoos there had recently stopped parasitizing meadow buntings, *Emberiza cioides*, and were starting to target a new host, the azure-winged magpie, *Cypanopica cyanus*.

ADAPTATIONS AND COUNTERADAPTATIONS ON THE FEN

The main feature of Davies & Brooke (1988) that distinguishes it from these other studies is its modular approach to understanding each of the common cuckoo's actions as she parasitizes a host nest. By asking explicit evolutionary questions and using carefully planned experiments, Davies & Brooke (1988) are able to dissect the natural history of cuckoo and host behaviour in temporal sequence, revealing the adaptive significance of each component step.

Before conducting any experiments, Davies & Brooke (1988) document some preliminary observations of the cuckoo's natural history. When a female cuckoo adds her egg to a host clutch, she

does so during the host's own laying period, before the clutch is complete and incubation begun. She visits her target nest in the afternoon, removes one of the host's own eggs and in its place swiftly lays an egg of her own, which closely resembles the reed warbler's own eggs in size, colour and patterning. Davies & Brooke (1988) report the natural parasitism rate of reed warblers at their study site on Wicken Fen and then determine that these hosts reject real cuckoo eggs at about 19% of parasitized nests.

To investigate exactly how cuckoos are able to sneak so many of their eggs past their hosts, Davies & Brooke (1988) describe how they play the part of the cuckoo themselves by adding model eggs to host nests. By parasitizing nests in their experiments before the host had begun laying, or without first removing a host egg, or early in the morning, or by lingering at the nest (by leaving a stuffed cuckoo nearby), or by 'laying' a nonmimetic model egg that was either larger than host eggs or painted not to resemble them, Davies & Brooke (1988) sequentially measure the fitness value of each of the cuckoo's actions during parasitism.

The experiments show that several aspects of cuckoo behaviour (egg mimicry, afternoon laying, small eggs and rapid visits) function to deceive hosts into accepting the cuckoo egg in their clutch while other behaviours (such as the removal of a host egg) probably benefit the young cuckoo by improving the efficiency of incubation and by sparing the nestling the effort of evicting another host egg or chick after hatching. The removed host egg may also serve as a 'free meal' for the female cuckoo, replenishing her energy and calcium stores and perhaps allowing her to lay more eggs. The experiments further show that, in response to cuckoo parasitism, hosts have evolved egg discrimination and are more inclined to reject eggs in reaction to the sight of a cuckoo near the nest. Finally, Davies & Brooke (1988) turn their attention to the nestling stage. By cross-fostering foreign dunnock, *Prunella modularis*, chicks into the nests of reed warblers, Davies & Brooke (1988) demonstrate that reed warbler parents fail to discriminate against chicks unlike their own (Fig. 2). They also present reed warbler parents with a simultaneous choice between feeding a cuckoo nestling and feeding a brood of host young and find that reed warblers do not favour cuckoo chicks over their own. These experimental results are interpreted alongside a comparative survey of host nestling mimicry by brood parasites.

In their overall interpretation of these simple field experiments, Davies & Brooke (1988) make (at least) four conceptual contributions to the field that have strongly influenced work carried out in subsequent years.

Recognition Costs

First, Davies & Brooke (1988) show that host defences are costly because hosts incur rejection costs when they remove an egg from their nests. Although Rothstein (1982) discussed the concept of rejection costs in some detail, Davies & Brooke (1988) were the first to quantify them empirically and to show that the rejections costs come in two forms. They may be the result of a recognition error, and thus the mistaken removal of a host egg, or of an ejection cost, namely damage sustained by host eggs while the alien egg is being forcibly removed from the nest. Not surprisingly, Davies & Brooke (1988) show that recognition costs are highest when hosts are faced with mimetic model eggs. Even so, Davies & Brooke (1988) find that there are limits on the extent of host gullibility. Reed warblers are not fooled into mistakenly rejecting one of their own eggs when they are shown a cuckoo mount near the nest. In subsequent work, Davies & Brooke (1989a, b) further developed their ideas about rejection costs, this time extending their analysis to include a range of parasitized and naïve hosts. In the second of these studies (1989b), Davies & Brooke provide a model of how recognition costs could lead to the acceptance of parasitic eggs,

Figure 2. Cuckoos versus reed warblers at the nestling stage. In contrast to the sophisticated egg mimicry exhibited by common cuckoos, *Cuculus canorus,* at the egg-laying stage, cuckoo nestlings are not mimetic. Despite this, reed warbler, *Acrocephalus scirpaceus,* hosts do not reject them. The puzzling lack of adaptation and counteradaptation at the nestling stage led Davies & Brooke (1988) to propose a new explanation for why reed warblers are good at discriminating against cuckoo eggs but not cuckoo young (see text). Photo: D. Kjaer.

later confirmed in work by Karen Marchetti (1992) and Arnon Lotem and colleagues (Lotem et al. 1992). Recognition costs were more formally modelled and tested in a subsequent signal detection model (Davies et al. 1996).

Recognition costs are now a key part of our understanding of variation within and among host populations in their propensity to reject cuckoo eggs (Davies & Brooke 1989b; Soler et al. 2000, 2002; Røskaft et al. 2002; Stokke et al. 2002, 2007; Lahti 2005, 2006; Vikan et al. 2009). Sophisticated models, incorporating the appearance of cuckoo and host eggs, host recognition ability and host learning, have been developed to predict whether, given a certain level of parasitism, a host should accept or reject a foreign egg (Stokke et al. 2007). Davies & Brooke (1988) use recognition costs to explain why hosts accept a cuckoo chick (Fig. 2; see Chick Rejection below), providing a starting point for predicting the conditions under which nestling ejection might evolve (Langmore et al. 2009). Quantifying the psychological constraints on recognition and the consequent risk of costly error remains an active area of research today (e.g. Shizuka & Lyon 2010; Spottiswoode & Stevens 2010).

Selection for Egg Mimicry by Second Cuckoos

The second conceptual contribution of Davies & Brooke (1988) is the proposal, and then testing, of a new hypothesis for the

evolution of egg mimicry (Fig. 1). Davies & Brooke (1988) suggest that a female cuckoo should target other cuckoo eggs that might already be present in a host nest for removal during parasitism, so as to prevent their own offspring from being evicted by another cuckoo nestling in due course. In this way, cuckoos themselves might select for cuckoo eggs that resemble host eggs because these would more easily escape discrimination by a second cuckoo visiting the nest. Davies & Brooke (1988) find little support for this hypothesis from their own experiments and acknowledge that selection by second cuckoos could anyway never be as strong as host discrimination. Nevertheless, the idea was embraced by the Brookers (1989) as an explanation for why Horsfield's bronze-cuckoos lay mimetic eggs that are never rejected by their superb fairy-wren, *Malurus cyaneus*, hosts, although it has not since withstood empirical testing (Langmore & Kilner 2009). As the evolutionary analysis of interactions between brood parasites and their hosts expands to include more species, it may yet be discovered that discrimination by brood parasites can play a key role in selecting for egg mimicry.

Frontline Defences

The third innovation of Davies & Brooke (1988) is the idea that host rejection behaviour can be influenced by environmental information, a revolutionary notion that had never before been tested. In the spirit of previous aggression studies employing stuffed cuckoos (e.g. Edwards et al. 1949), Davies & Brooke (1988) present a stuffed common cuckoo (or a control stuffed jackdaw) at host nests to determine whether reed warblers are more likely to reject cuckoo eggs when they see a cuckoo in the vicinity. Both the cuckoo and jackdaw models were equally likely to be mobbed on the nest, but egg rejection by hosts went up slightly upon seeing a cuckoo. Although mobbing behaviour was not the focus of these experiments, this approach set the stage for research on so-called front-line defences and the role of social learning in the acquisition of host defences, a line of research that is currently very active (reviewed in Feeney et al. 2012).

For example, recent field experiments by Welbergen & Davies (2009) showed that reed warblers can effectively defend themselves against parasitism by mobbing common cuckoos. In parts of Wicken Fen where the risk of parasitism was high, reed warblers that mobbed a stuffed cuckoo were less likely to be parasitized by cuckoos than reed warblers that did not mob. The experiments also revealed that reed warblers modify their mobbing behaviour according to local parasitism risk, indicating that mobbing behaviour is a phenotypically flexible trait. Do reed warblers learn about cuckoo threats from their neighbours? In a separate series of experiments, Davies & Welbergen (2009) showed that reed warblers use social learning to bolster nest defence. Reed warblers increased their response to cuckoos if they observed their neighbours mobbing a cuckoo but not a parrot (a benign control). To beat these sophisticated host defences, cuckoos may have evolved an alternative guise. Female common cuckoos typically have grey plumage but some females have rufous coloration. Thorogood & Davies (2012) demonstrated that reed warblers, upon seeing their neighbours mob a cuckoo model, increased their own mobbing behaviour but only to the cuckoo morph (grey or rufous) they observed their neighbours attack. This result suggests that frequency-dependent social information has resulted in the evolution of polymorphic plumage in cuckoos, which permits rare forms to escape detection.

Chick Rejection

Finally, Davies & Brooke (1988) introduce a new idea about the perplexing lack of common cuckoo chick rejection by hosts (Fig. 2).

One of the enduring puzzles surrounding host defences against common cuckoos is that many hosts exhibit exquisite adaptations when defending their clutch against the addition of a foreign egg (Fig. 1) yet switch to behaving in a peculiarly maladaptive fashion once the cuckoo hatches (Fig. 2). The hosts seemingly lose all fastidiousness over their allocation of parental care to instead provision the grotesque chick in their nest, which has killed all of the hosts' own young by throwing them out of the nest. Dawkins & Krebs (1979) suggested that this is because hosts are so beguiled by the supernormal begging of the common cuckoo nestling that they are incapable of resisting its demands for food. However, Davies & Brooke (1988) find no evidence to support this idea. First, they show that host reed warblers are unable to discriminate against a foreign dunnock nestling placed in their nest even though these dunnocks lacked a supernormal begging display. Second, Davies & Brooke (1988) find that the cuckoo nestling's begging is not so supernormal after all. When hosts were given the opportunity to make a simultaneous choice between feeding a cuckoo chick or their own brood, they simply fed whichever young begged most vigorously and showed no preference for the cuckoo. Subsequent field experiments have reinforced Davies & Brooke's (1988) conclusion that common cuckoo chicks are not supernormal beggars (Brooke & Davies 1989; Kilner et al. 1999).

So why don't hosts discriminate against common cuckoo nestlings (Fig. 2)? One possibility is evolutionary lag; hosts simply have yet to evolve this line of defence. Davies & Brooke (1988) advance a novel and insightful adaptive explanation as well. First, they point out that hosts of evictor parasites, like the common cuckoo, benefit much more by rejecting eggs early in the breeding season, thereby saving their brood from eviction, than by rejecting chicks much later. Therefore, it is not surprising that reed warblers discriminate against eggs rather than nestlings. To support this line of reasoning further, Davies & Brooke (1988) compile comparative data that suggest that brood parasitic nestlings are only mimetic (and presumably therefore discriminated against) when reared alongside host young. Chick rejection may thus be adaptive among hosts of brood parasites that, unlike the common cuckoo, do not evict their nestmates. Davies & Brooke (1988) argue that this is because the benefits of rejecting parasitic young are so much greater in these cases: these hosts can still rear their own remaining offspring once they have done away with the parasite.

Low as the benefits of chick rejection may be for hosts of the common cuckoo, the benefits are still greater than when there is no chick rejection at all. To explain the complete lack of discrimination against cuckoo nestlings by reed warblers, Davies & Brooke (1988) suggest that the costs of recognizing the cuckoo nestling must exceed any benefits thus gained. Recognizing an alien chick, which rapidly changes in appearance as it grows in the nest, may be considerably more complex than recognizing a foreign egg. Moreover, the cost of mistakenly rejecting a host's own chick is considerably higher than the cost of mistakenly rejecting a host's own egg. For these reasons, Davies & Brooke (1988) hypothesize, it may be more challenging to evolve a template for chick rejection than for egg rejection.

In 1988, Davies and Brooke could only speculate what form such costs might take. Their ideas were fleshed out more fully by Arnon Lotem and colleagues. Lotem et al. (1992) proposed that hosts learn the appearance of their own clutch during their first breeding attempt and thereafter reject any eggs that appear odd by comparison. However, Lotem (1993) showed that a similar mechanism for learned recognition cannot work at the nestling stage. Any host that was unlucky enough to be parasitized in its first breeding attempt would misimprint on the lone cuckoo in its nest and thereafter mistakenly reject its own nestlings. This potential recognition cost, arising as a consequence of misimprinting, would

outweigh any benefit of discrimination and chick rejection could never evolve (Lotem 1993).

Recent research on the bronze-cuckoos (*Chalcites* spp.) and their hosts has uncovered the type of natural history shock that makes working on brood parasites so rewarding. Contrary to everyone's expectations, some hosts of evictor cuckoos can indeed reject nestling parasites, either by abandonment (Langmore et al. 2003) or by physically grasping the cuckoo chick and flinging it from the nest (Sato et al. 2010; Tokue & Ueda 2010). Furthermore, chick recognition is learned (Langmore et al. 2009; Shizuka & Lyon 2010) and hosts have mechanisms in place to ensure there is no risk of misimprinting (Shizuka & Lyon 2010). Just as there are adaptations and counteradaptations at the egg stage in reed warblers and common cuckoos, so there are adaptations and counteradaptations at the nestling stage in bronze-cuckoos and their hosts. Discrimination by hosts has selected for cuckoo nestlings that mimic host young, either in their appearance (Langmore et al. 2011) or in their begging calls (Langmore et al. 2003, 2008). These findings thus give us a new puzzle to solve: why do some cuckoo hosts apparently specialize in rejecting nestlings while others seem to focus on rejecting eggs? The kind of cost–benefit analyses introduced by Davies & Brooke (1988) for understanding the evolution of common cuckoo nestling rejection will no doubt underpin any attempts to answer this question in the future.

FUTURE PROSPECTS

The enduring value of Davies & Brooke (1988) lies in its elegant identification of adaptations and counteradaptations, where the agent of selection is known and where the fitness consequences of the interspecific interaction can be quantified for both parties. Davies & Brooke (1988) show that the fitness costs of parasitism can be quantified for hosts because cuckoo chicks evict host young from the nest or otherwise contribute to their deaths. Likewise, the fitness costs for cuckoos can be measured because host defences cause the certain death of cuckoo offspring. Although simple to understand, these properties are rare in systems exposed to detailed evolutionary analysis and are therefore particularly valuable. We conclude by highlighting just three of several possible ways in which future research areas might exploit this advantage.

Genomics

Genomics has recently exploded into field biology, yielding new insights into the genetic basis of adaptations in nature. Traits that have coevolved have contributed substantially to this rapidly growing area, particularly those arising from coevolution between predators and prey (Abzhanov et al. 2004; Barrett et al. 2008; Feldman et al. 2009). In these cases, adaptive traits are relatively simple to identify for genetic analysis. The adaptations and counteradaptations exhibited by brood parasites and their hosts are thus ripe for equivalent genomic analysis (Edwards 2012). Furthermore, several of these adaptations and counteradaptations involve colourful traits. Recent studies show that coloration in vertebrates is a highly tractable trait for studying the genetic basis of adaptation (e.g. Mundy et al. 2004; Gratten et al. 2008; Linnen et al. 2009). This is especially true for melanic traits, such as bronze-cuckoo chick adaptations involving variation in nestling skin colour (Langmore et al. 2011), because variation can be easily quantified and there is detailed knowledge of underlying genetic networks from work on mice and chickens (Mundy 2005; Hoekstra et al. 2006). The genetics of adaptation may also be revealed by investigating eggshell pigmentation, which is highly conserved across birds yet remarkably variable in many brood parasite–host systems. Preliminary studies using the chicken genome have begun to pinpoint the genes

involved in eggshell coloration (Kilner 2006), laying the groundwork for active research on the genetic changes responsible for egg colour and pattern polymorphisms in brood parasite–host systems.

A detailed investigation of the location of the genes involved in cuckoo egg coloration will help us understand the evolutionary consequences of adaptations for parasitism. Revealing the genetics underlying egg coloration is key to understanding how host specificity is maintained, particularly in the face of gene flow caused by promiscuous mating by males across host-specific lineages (Marchetti et al. 1998; Gibbs et al. 2000). The predominant hypothesis is that the genes controlling egg phenotype are confined to the W chromosome in brood parasites (Davies 2000). Restricting these genes to the female line in this way effectively makes them immune to introgression from the male genome. However, there is no direct evidence to support this view and in fact some evidence to suggest it is unlikely (Fossøy et al. 2011). For example, recent evidence from cuckoo finches, *Anomalospiza imberbis*, shows that egg phenotypes can evolve extraordinarily rapidly (Spottiswoode & Stevens 2012), which is unlikely to be the case if they are confined to the W chromosome (Berlin & Ellegren 2004). Furthermore, the shiny cowbird, *Molothrus bonariensis*, from Argentina lays polymorphic eggs but the genes controlling this egg polymorphism are located on the autosomes (Mahler et al. 2008). Describing the natural history of brood parasite genomes is clearly crucial for solving these puzzles (Edwards 2012).

In short, the genomic analyses of cuckoo and host adaptations and counteradaptations have the potential to address several major questions in evolutionary biology. For example, genomic research will allow us to determine whether similar genetic changes have occurred in multiple brood parasite–host lineages and to discover which parts of the genome are particularly likely to generate new adaptive phenotypes (Hoekstra & Coyne 2007). Similarly, an important question in evolutionary biology is whether the genetic basis of adaptation at the microevolutionary level is recapitulated in macroevolution (Mundy et al. 2004; Pointer & Mundy 2008), a question that can be addressed through comparative analyses of closely related brood parasites.

Sensory Ecology

The interactions between brood parasites and their hosts lend themselves ideally to analysis with new techniques from sensory ecology. Host visual systems, for example, have played a crucial role in the evolution of sophisticated mimicry by brood parasites at three stages of the parasitism sequence in diverse systems: as parasites infiltrate host nests, at the egg stage and at the nestling stage (reviewed in Langmore & Spottiswoode 2012). Avian nests provide a relatively constant microenvironment for the perception of visual and auditory information, making it relatively straightforward to quantify stimuli from eggs and chicks that are perceived by host sensory systems. Moreover, the widespread availability of spectrophotometers and digital cameras, combined with advanced models of avian vision, have transformed the way we can evaluate colour and pattern mimicry through the eyes of host birds (Bennett & Théry 2007; Stevens 2011; Stoddard 2012). Visual modelling has recently revealed previously overlooked properties of egg and nestling mimicry, selected by the way avian host eyes sense colour and patterning (Avilés 2008; Spottiswoode & Stevens 2010; Langmore et al. 2011; Stoddard & Stevens 2010, 2011), and has enabled the quantification of coevolutionary trajectories between hosts and brood parasites in ways that were previously impossible.

In many brood parasite–host systems, visual trickery has evolved not only in response to host defences but also to exploit pre-existing biases in the host. This form of 'tuning', which taps into the host's sensory preferences, often helps the parasite chick to

elicit parental care from its host parents (Davies 2011; Langmore & Spottiswoode 2012). Evaluating potentially 'supernormal' visual stimuli through the eyes of hosts has shed light on how host chicks successfully exploit their foster parents (Tanaka et al. 2011).

Auditory mimicry and exploitation are often important features of parasite–host coevolution (Langmore et al. 2003; Grim 2006) and recent bioacoustic modelling has led to novel insights about the mechanism and function of parasite begging calls (Ranjard et al. 2010). It would be interesting in future work to develop more sophisticated models of sensory processing that take into account higher order cognitive processing of the visual and auditory information detected by the bird eye and ear. These could be usefully deployed to determine more precisely how hosts select for mimicry of egg patterns or begging calls, for example, or how hosts integrate mimetic cues from different sensory modalities.

Perhaps a different challenge for future work in sensory ecology will be to investigate instances where mimicry by the brood parasite does not appear to be perfect. Is imperfect mimicry nevertheless good enough to beat sensory detection by the host? Are there intrinsic constraints on the extent of mimicry that are independent of host senses? It will be fascinating to explore whether some brood parasites employ jack-of-all-trades mimicry (Sherratt 2002), thus permitting eggs or chicks to be sufficiently mimetic for multiple hosts. In addition, distinguishing between true mimicry and similarity, which can arise via common ancestry or from pre-existing preferences (see Grim 2005), remains an important goal for the future, and understanding both host and parasite sensory systems will be essential for this task.

Cognition

There is growing interest in the study of 'wild cognition', the sophisticated processing and use of information in behavioural decisions made by animals in nature. Experimental work with diverse species shows in general how selection from the social environment experienced by different species can account for variation exhibited in cognitive skills (e.g. Emery & Clayton 2004). Davies & Brooke (1988) show that brood parasites and their hosts potentially lend themselves well to this field of enquiry. Recognition defences against brood parasitism typically involve cognitive processing because the decision to reject foreign young is based on multiple sources of information, some of it remembered from past events. For example, Davies & Brooke (1988) themselves show that hosts change their response to foreign eggs when alerted to their presence by a stuffed cuckoo loitering near their nest. Furthermore, recent studies (Langmore et al. 2003, 2009) show that diverse cues from the nestling and the wider environment are integrated to inform host decisions about whether or not to reject cuckoo nestlings. We now know that hosts also draw on learned recognition templates to identify offspring in their nests (Lotem et al. 1995; Øien et al. 1995; Langmore et al. 2009; Shizuka & Lyon 2010). By capitalizing on increasing numbers of studies on marked host populations, we will be able to elucidate the cognitive rules underpinning rejection decisions in future experiments.

There are also considerable cognitive challenges involved in pursuing a parasitic lifestyle. Adult brood parasite females must remember where host nests are and when hosts started laying their eggs when choosing where to lay their egg (Reboreda et al. 1996). Some adult parasites even apparently draw on memories of whether or not their eggs were rejected by particular hosts to operate protection rackets, effectively forcing hosts to accept their eggs or else risk losing their entire clutch to future attack by the parasite (e.g. Hoover & Robinson 2007). It would be challenging but illuminating to determine the cognitive decisions involved in the brood parasite's egg-laying process.

State-of-the-art fMRI analysis of the cognitive processes undertaken by humans during decision making reveals that different parts of the brain are deployed for different cognitive tasks. We can fantasize that in future work we might be able to take this technology into the field and peer into the brain of the cuckoo as she decides where to lay her next egg or the reed warbler as it weighs up whether or not to remove a foreign egg from its nest. Davies & Brooke (1988) show us how the behaviour of brood parasites and their hosts can be explained by selection they exert on each other. Armed with this knowledge, we can now start to interpret the natural history of their genomes and their brains.

References

Abzhanov, A., Protas, M., Grant, B. R., Grant, P. R. & Tabin, C. J. 2004. *Bmp4* and morphological variation of beaks in Darwin's finches. *Science*, **305**, 1462–1465.

Avilés, J. M. 2008. Egg colour mimicry in the common cuckoo *Cuculus canorus* as revealed by modelling host retinal function. *Proceedings of the Royal Society B*, **275**, 2345–2352.

Baker, E. C. S. 1923. Cuckoo eggs and evolution. *Proceedings of the Zoological Society of London*, **1923**, 277–294.

Baldamus, E. 1892. *Das Leben der Europäischen Kuckucke*. Berlin: Parey.

Barrett, R. D. H., Rogers, S. M. & Schluter, D. 2008. Natural selection on a major armor gene in threespine stickleback. *Science*, **322**, 255–257.

Bechstein, J. M. 1791. *Gemeinnützige Naturgeschichte Deutschlands Bd. 2*. Leipzig: Crusius.

Bennett, A. T. D. & Théry, M. 2007. Avian color vision and coloration: multidisciplinary evolutionary biology. *The American Naturalist*, **169**, 1–6.

Berlin, S. & Ellegren, H. 2004. Chicken W: a genetically uniform chromosome in a highly variable genome. *Proceedings of the National Academy of Sciences, U.S.A.*, **101**, 15967–15969.

Blyth, E. 1835. Observations on the cuckoo. *Magazine of Natural History*, **8**, 325–340.

Brooke, M. de L. & Davies, N. 1989. Provisioning of nestling cuckoos *Cuculus canorus* by reed warbler *Acrocephalus scirpaceus* hosts. *Ibis*, **131**, 250–256.

Brooker, M. G. & Brooker, L. C. 1989. The comparative breeding behaviour of two sympatric cuckoos, Horsfield's bronze-cuckoo *Chrysococcyx basalis* and the shining bronze-cuckoo *C. lucidus*, in Western Australia: a new model of the evolution of egg morphology and host specificity in avian brood parasites. *Ibis*, **131**, 528–547.

Darwin, C. 1859. *The Origin of Species*. London: John Murray.

Davies, N. B. 2000. *Cuckoos, Cowbirds and Other Cheats*. London: T. & A.D. Poyser.

Davies, N. B. 2011. Cuckoo adaptations: trickery and tuning. *Journal of Zoology*, **284**, 1–14.

Davies, N. B. & Brooke, M. de L. 1988. Cuckoos versus reed warblers: adaptations and counteradaptations. *Animal Behaviour*, **36**, 262–284.

Davies, N. B. & Brooke, M. de L. 1989a. An experimental study of co-evolution between the cuckoo, *Cuculus canorus*, and its hosts. I. Host egg discrimination. *Journal of Animal Ecology*, **58**, 207–224.

Davies, N. B. & Brooke, M. de L. 1989b. An experimental study of co-evolution between the cuckoo, *Cuculus canorus*, and its hosts. II. Host egg markings, chick discrimination and general discussion. *Journal of Animal Ecology*, **58**, 225–236.

Davies, N. B. & Welbergen, J. A. 2009. Social transmission of a host defense against cuckoo parasitism. *Science*, **324**, 1318–1320.

Davies, N. B., Brooke, M. de L. & Kacelnik, A. 1996. Recognition errors and probability of parasitism determine whether reed warblers should accept or reject cuckoo eggs. *Proceedings of the Royal Society B*, **263**, 925–931.

Dawkins, R. & Krebs, J. 1979. Arms races between and within species. *Proceedings of the Royal Society B*, **205**, 489–511.

Edwards, G., Hosking, E. & Smith, S. 1949. Reactions of some passerine birds to a stuffed cuckoo. *British Birds*, **42**, 13–19.

Edwards, S. V. 2012. Afterward [on genetics and the evolutionary history of avian brood parasitism, a response to chapter by Langmore and Spottiswoode]. In: *Host Manipulation by Parasites* (Ed. by D. P. Hughes, J. Brodeur & F. Thomas), pp. 116–118. New York: Oxford University Press.

Emery, N. J. & Clayton, N. S. 2004. The mentality of crows: convergent evolution of intelligence in corvids and apes. *Science*, **306**, 1903–1907.

Feeney, W. E., Welbergen, J. A. & Langmore, N. E. 2012. The frontline of avian brood parasite-host coevolution. *Animal Behaviour*, **84**, 3–12.

Feldman, C. R., Brodie, E. D., Jr., Brodie, E. D., III & Pfrender, M. E. 2009. The evolutionary origins of beneficial alleles during the repeated adaptation of garter snakes to deadly prey. *Proceedings of the National Academy of Sciences, U.S.A.*, **106**, 13415–13420.

Fossøy, F., Antonov, A., Moksnes, A., Røskaft, E., Vikan, J. R., Møller, A. P., Shykoff, J. A. & Stokke, B. G. 2011. Genetic differentiation among sympatric cuckoo host races: males matter. *Proceedings of the Royal Society B*, **278**, 1639–1645.

Gibbs, H. L., Sorenson, M. D., Marchetti, K., Brooke, M. de L., Davies, N. B. & Nakamura, H. 2000. Genetic evidence for female host-specific races of the common cuckoo. *Nature*, **407**, 183–186.

Gratten, J., Wilson, A. J., McRae, A. F., Beraldi, D., Visscher, P. M., Pemberton, J. M. & Slate, J. 2008. A localized negative genetic correlation constrains microevolution of coat color in wild sheep. *Science*, **319**, 318–320.

Grim, T. 2005. Mimicry vs. similarity: which resemblances between brood parasites and their hosts are mimetic and which are not? *Biological Journal of the Linnean Society*, **84**, 69–78.

Grim, T. 2006. The evolution of nestling discrimination by hosts of parasitic birds: why is rejection so rare? *Evolutionary Ecology Research*, **8**, 785–802.

Hett, W. S. 1936. *Aristotle: Minor Works. On Marvellous Things Heard*. London: Heinemann.

Hoekstra, H. E. & Coyne, J. A. 2007. The locus of evolution: evo devo and the genetics of adaptation. *Evolution*, **61**, 995–1016.

Hoekstra, H. E., Hirschmann, R. J., Bundey, R. A., Insel, P. A. & Crossland, J. P. 2006. A single amino acid mutation contributes to adaptive beach mouse color pattern. *Science*, **313**, 101–104.

Hoover, J. P. & Robinson, S. K. 2007. Retaliatory mafia behavior by a parasitic cowbird favors host acceptance of parasitic eggs. *Proceedings of the National Academy of Sciences, U.S.A.*, **104**, 4479–4483.

Kilner, R. M. 2006. The evolution of egg colour and patterning in birds. *Biological Reviews*, **81**, 383–406.

Kilner, R., Noble, D. & Davies, N. 1999. Signals of need in parent-offspring communication and their exploitation by the common cuckoo. *Nature*, **397**, 667–672.

Lahti, D. C. 2005. Evolution of bird eggs in the absence of cuckoo parasitism. *Proceedings of the National Academy of Sciences, U.S.A.*, **102**, 18057–18062.

Lahti, D. C. 2006. Persistence of egg recognition in the absence of cuckoo brood parasitism: pattern and mechanism. *Evolution*, **60**, 157–168.

Langmore, N. & Kilner, R. 2009. Why do Horsfield's bronze-cuckoo *Chalcites basalis* eggs mimic those of their hosts? *Behavioral Ecology and Sociobiology*, **63**, 1127–1131.

Langmore, N. E. & Spottiswoode, C. N. 2012. Visual trickery in avian brood parasites. In: *Host Manipulation by Parasites* (Ed. by D. P. Hughes, J. Brodeur & F. Thomas). New York: Oxford University Press.

Langmore, N. E., Hunt, S. & Kilner, R. M. 2003. Escalation of a coevolutionary arms race through host rejection of brood parasitic young. *Nature*, **422**, 157–160.

Langmore, N. E., Maurer, G., Adcock, A. J. & Kilner, R. M. 2008. Socially acquired host-specific mimicry and the evolution of host races in Horsfield's bronze-cuckoo *Chalcites basalis*. *Evolution*, **62**, 1689–1699.

Langmore, N. E., Cockburn, A., Russell, A. F. & Kilner, R. M. 2009. Flexible cuckoo chick-rejection rules in the superb fairy-wren. *Behavioral Ecology*, **20**, 978–984.

Langmore, N. E., Stevens, M., Maurer, G., Heinsohn, R., Hall, M. L., Peters, A. & Kilner, R. M. 2011. Visual mimicry of host nestlings by cuckoos. *Proceedings of the Royal Society B*, **278**, 2455–2463.

Linnen, C. R., Kingsley, E. P., Jensen, J. D. & Hoekstra, H. E. 2009. On the origin and spread of an adaptive allele in deer mice. *Science*, **325**, 1095–1098.

Lotem, A. 1993. Learning to recognize nestlings is maladaptive for cuckoo *Cuculus canorus* hosts. *Nature*, **362**, 743–745.

Lotem, A., Nakamura, H. & Zahavi, A. 1992. Rejection of cuckoo eggs in relation to host age: a possible evolutionary equilibrium. *Behavioral Ecology*, **3**, 128–132.

Lotem, A., Nakamura, H. & Zahavi, A. 1995. Constraints on egg discrimination and cuckoo host coevolution. *Animal Behaviour*, **49**, 1185–1209.

Lottinger, A. J. 1776. *Der Kukuk, auf eigene Erfahrung gegründete Nachrichten über die Natur-Geschichte dieses wunderbaren Vogels*. Translation from the French edition 1775. Strassburg: König.

Mahler, B., Confalonieri, V. A., Lovette, I. J. & Reboreda, J. C. 2008. Eggshell spotting in brood parasitic shiny cowbirds (*Molothrus bonariensis*) is not linked to the female sex chromosome. *Behavioral Ecology and Sociobiology*, **62**, 1193–1199.

Marchetti, K. 1992. Costs to host defence and the persistence of parasitic cuckoos. *Proceedings of the Royal Society B*, **248**, 41–45.

Marchetti, K., Nakamura, H. & Gibbs, H. L. 1998. Host-race formation in the common cuckoo. *Science*, **282**, 471–472.

Moksnes, A. & Røskaft, E. 1988. Responses of fieldfares *Turdus pilaris* and bramblings *Fringilla montifringilla* to experimental parasitism by the cuckoo *Cuculus canorus*. *Ibis*, **130**, 535–539.

Moksnes, A., Røskaft, E., Rudolfsen, G., Skjelseth, S., Stokke, B. G., Kleven, O., Gibbs, H. L., Honza, M., Taborsky, B. & Teuschl, Y. 2008. Individual female common cuckoos *Cuculus canorus* lay constant egg types but egg appearance cannot be used to assign eggs to females. *Journal of Avian Biology*, **39**, 238–241.

Mundy, N. I. 2005. A window on the genetics of evolution: MC1R and plumage colouration in birds. *Proceedings of the Royal Society B*, **272**, 1633–1640.

Mundy, N. I., Badcock, N. S., Hart, T., Scribner, K., Janssen, K. & Nadeau, N. J. 2004. Conserved genetic basis of a quantitative plumage trait involved in mate choice. *Science*, **303**, 1870–1873.

Nakamura, H. 1990. Brood parasitism by the cuckoo *Cuculus canorus* in Japan and the start of new parasitism on the azure-winged magpie *Cyanopica cyana*. *Japanese Journal of Ornithology*, **39**, 1–18.

Newton, A. 1896. *A Dictionary of Birds*. London: A. & C. Black.

Øien, I. J., Moksnes, A. & Røskaft, E. 1995. Evolution of variation in egg color and marking pattern in European passerines: adaptations in a coevolutionary arms race with the cuckoo, *Cuculus canorus*. *Behavioral Ecology*, **6**, 166–174.

Payne, R. B. 1977. The ecology of brood parasitism in birds. *Annual Review of Ecology and Systematics*, **8**, 1–28.

Pointer, M. A. & Mundy, N. I. 2008. Testing whether macroevolution follows microevolution: are colour differences among swans (*Cygnus*) attributable to variation at the MC1R locus? *BMC Evolutionary Biology*, **8**, 249–256.

Ranjard, L., Anderson, M. G., Rayner, M. J., Payne, R. B., McLean, I., Briskie, J. V., Ross, H. A., Brunton, D. H., Woolley, S. M. N. & Hauber, M. E. 2010. Bioacoustic distances between the begging calls of brood parasites and their host species: a comparison of metrics and techniques. *Behavioral Ecology and Sociobiology*, **64**, 1915–1926.

Reboreda, J. C., Clayton, N. S. & Kacelnik, A. 1996. Species and sex differences in hippocampus size in parasitic and non-parasitic cowbirds. *NeuroReport: International Journal for Rapid Communications of Research in Neuroscience*, **7**, 505–508.

Rensch, B. 1925. Verhalten von Singvögeln bei Änderung des Geleges. *Ornithologische Monatsschrift*, **33**, 169–173.

Rey, E. 1892. *Altes und Neues aus dem Haushalte des Kuckucks*. Leipzig: R. Freese.

Røskaft, E., Moksnes, A., Stokke, B. G., Moskát, C. & Honza, M. 2002. The spatial habitat structure of host populations explains the pattern of rejection behavior in hosts and parasitic adaptations in cuckoos. *Behavioral Ecology*, **13**, 163–168.

Rothstein, S. I. 1975. An experimental and teleonomic investigation of avian brood parasitism. *Condor*, **77**, 250–271.

Rothstein, S. I. 1982. Mechanisms of avian egg recognition: which egg parameters elicit responses by rejecter species? *Behavioral Ecology and Sociobiology*, **11**, 229–239.

Sato, N. J., Tokue, K., Noske, R. A., Mikami, O. K. & Ueda, K. 2010. Evicting cuckoo nestlings from the nest: a new anti-parasitism behaviour. *Biology Letters*, **6**, 67–69.

Schulze-Hagen, K., Stokke, B. G. & Birkhead, T. R. 2009. Reproductive biology of the European cuckoo *Cuculus canorus*: early insights, persistent errors and the acquisition of knowledge. *Journal of Ornithology*, **150**, 1–16.

Sherratt, T. N. 2002. The evolution of imperfect mimicry. *Behavioral Ecology*, **13**, 821–826.

Shizuka, D. & Lyon, B. E. 2010. Coots use hatch order to learn to recognize and reject conspecific brood parasitic chicks. *Nature*, **463**, 223–226.

Soler, J. J., Soler, M. & Møller, A. P. 2000. Host recognition of parasite eggs and the physical appearance of host eggs: the magpie and its brood parasite the great spotted cuckoo. *Etologia*, **8**, 9–16.

Soler, M., Martín-Vivaldi, M. & Pérez-Contreras 2002. Identification of the sex responsible for recognition and the method of ejection of parasitic eggs in some potential common cuckoo hosts. *Ethology*, **108**, 1093–1101.

Spottiswoode, C. N. & Stevens, M. 2010. Visual modeling shows that avian host parents use multiple visual cues in rejecting parasitic eggs. *Proceedings of the National Academy of Sciences, U.S.A.*, **107**, 8672–8676.

Spottiswoode, C. N. & Stevens, M. 2012. Host-parasite arms races and rapid changes in bird egg appearance. *The American Naturalist*, **179**, 633–648.

Stevens, M. 2011. Avian vision and egg colouration: concepts and measurements. *Avian Biology Research*, **4**, 168–184.

Stoddard, M. C. 2012. Mimicry and masquerade from the avian visual perspective. *Current Zoology*, **58**, 630–648.

Stoddard, M. C. & Stevens, M. 2010. Pattern mimicry of host eggs by the common cuckoo, as seen through a bird's eye. *Proceedings of the Royal Society B*, **277**, 1387–1393.

Stoddard, M. C. & Stevens, M. 2011. Avian vision and the evolution of egg color mimicry in the common cuckoo. *Evolution*, **65**, 2004–2013.

Stokke, B. G., Honza, M., Moksnes, A., Roskaft, E. & Rudolfsen, G. 2002. Costs associated with recognition and rejection of parasitic eggs in two European passerines. *Behaviour*, **139**, 629–644.

Stokke, B. G., Takasu, F., Moksnes, A. & Røskaft, E. 2007. The importance of clutch characteristics and learning for antiparasite adaptations in hosts of avian brood parasites. *Evolution*, **61**, 2212–2228.

Swynnerton, C. M. F. 1918. Rejections by birds of eggs unlike their own: with remarks on some of the cuckoo problems. *Ibis*, **60**, 127–154.

Tanaka, K. D., Morimoto, G., Stevens, M. & Ueda, K. 2011. Rethinking visual supernormal stimuli in cuckoos: visual modeling of host and parasite signals. *Behavioral Ecology*, **22**, 1012–1019.

Thorogood, R. & Davies, N. B. 2012. Cuckoos combat socially transmitted defenses of reed warbler hosts with a plumage polymorphism. *Science*, **337**, 578–580.

Tokue, K. & Ueda, K. 2010. Mangrove gerygones *Gerygone laevigaster* eject little bronze-cuckoo *Chalcites minutillus* hatchlings from parasitized nests. *Ibis*, **152**, 835–839.

Vikan, J. R., Stokke, B. G., Fossøy, F., Jackson, C., Huhta, E., Rutila, J., Moksnes, A. & Røskaft, E. 2009. Fixed rejection responses to single and multiple experimental parasitism in two *Fringilla* hosts of the common cuckoo. *Ethology*, **115**, 840–850.

Welbergen, J. A. & Davies, N. B. 2009. Strategic variation in mobbing as a front line defence against cuckoo parasitism. *Current Biology*, **19**, 235–240.

Williams, G. C. 1966. *Adaptation and Natural Selection: a Critique of Some Current Evolutionary Thought*. Princeton, New Jersey: Princeton University Press.