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60 YEARS OF ANIMAL BEHAVIOUR

Anniversary Essay

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

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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.

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

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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) groundbreaking 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