THE ROYAL SOCIETY
PUBLISHING

The coevolutionary biology of brood parasitism: a call for integration

Rose Thorogood[1,2,3], Claire N. Spottiswoode[3,4], Steven J. Portugal[5] and Ros Gloag[6]

[1]Helsinki Institute of Life Science, University of Helsinki, Helsinki 00014, Finland
[2]Research Program in Organismal and Evolutionary Biology, Faculty of Environmental and Biological Sciences, University of Helsinki, Helsinki 00014, Finland
[3]Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK
[4]FitzPatrick Institute of African Ornithology, DST-NRF Centre of Excellence, University of Cape Town, Rondebosch 7701, South Africa
[5]School of Biological Sciences, Royal Holloway University of London, Egham, Surrey TW20 0EX, UK
[6]School of Life and Environmental Sciences, University of Sydney, Sydney 2006, Australia

RT, 0000-0001-5010-2177; SJP, 0000-0002-2438-2352; RG, 0000-0002-2037-4267

Obligate brood-parasitic cheats have fascinated natural historians since ancient times. Passing on the costs of parental care to others occurs widely in birds, insects and fish, and often exerts selection pressure on hosts that in turn evolve defences. Brood parasites have therefore provided an illuminating system for researching coevolution. Nevertheless, much remains unknown about how ecology and evolutionary history constrain or facilitate brood parasitism, or the mechanisms that shape or respond to selection. In this special issue, we bring together examples from across the animal kingdom to illustrate the diverse ways in which recent research is addressing these gaps. This special issue also considers how research on brood parasitism may benefit from, and in turn inform, related fields such as social evolution and immunity. Here, we argue that progress in our understanding of coevolution would benefit from the increased integration of ideas across taxonomic boundaries and across Tinbergen's Four Questions: mechanism, ontogeny, function and phylogeny of brood parasitism. We also encourage renewed vigour in uncovering the natural history of the majority of the world's brood parasites that remain little-known. Indeed, it seems very likely that some of nature's brood parasites remain entirely unknown, because otherwise we are left with a puzzle: if parental care is so costly, why is brood parasitism not more common?

This article is part of the theme issue 'The coevolutionary biology of brood parasitism: from mechanism to pattern'.

1. Introduction

Parental care is a key aspect of the life history of many animals [1], including our own species. It is perhaps not surprising then that we find it hard to forget the sight of a small bird devoting its parental attention to a noisy and monstrously large parasitic cuckoo chick that is so clearly, to our eyes, an imposter in the nest. This reproductive strategy of having one's offspring reared by another species—brood parasitism—has fascinated naturalists and other curious minds for centuries [2]. For example, Confucian texts from the sixth century BC explained the reproductive habits of common cuckoos *Cuculus canorus* (the eponymous brood-parasitic bird) as an opportunity for hosts to pay homage to an exemplary ruler [3]. In the light of evolutionary theory (e.g. [4]), however, we now know that the 'exemplary ruler' is a cheat, parasitizing the parental investment of host species. Such cheats have been of particular scientific interest as striking and tractable examples of coevolution, the process through which two or more species reciprocally affect each other's evolution [4]: we can readily identify real selection pressures in the wild, and test them with field experiments. The hallmarks of coevolution are its dynamism and its capacity to generate novelty, as

each party experiences continually changing selection from a nimble and ever-changing partner [5]. Our appreciation for its power to shape beautiful adaptations in antagonists and their victims comes in no small part from studies of brood parasites and their hosts [6].

Where do we find brood parasites in nature? Parental care strategies evolve when the fitness benefits to parents of caring for their young outweigh the costs in terms of energy and residual reproductive value [7]. These costs expose parents to cheating, because individuals that can achieve the benefits of parental care without paying the concomitant costs are favoured by natural selection. It follows then that we might expect obligate brood parasitism to evolve wherever we see parental care.

Parental care is particularly prevalent in birds, and avian brood parasitism has received the lion's share of research effort into brood parasites (for reviews, see [6,8–10]). Obligate interspecific brood parasitism is found in approximately 1% of all birds, has evolved independently seven times and can be found on every continent except Antarctica [6]. Evolutionary transitions to brood parasitism in birds vary from very ancient (e.g. approx. 26 Myr ago in *Indicator* honeyguides [11]) to an order of magnitude more recent (e.g. the black-headed duck *Heteronetta atricapilla*, *Molothrus* cowbirds [12]). Typically, avian brood parasites lay their eggs in the nests of host species to take advantage of both incubation and chick-rearing behaviour. They may exploit the behaviour of a single pair of hosts (parents) or of a unit of cooperatively breeding hosts (parents plus helpers) (e.g. [13], and see [14] in this issue). Parasites have a suite of adaptations across the life stages that allow successful exploitation of hosts: adult females track the nesting progress of hosts and lay eggs at the appropriate time to ensure optimal development, eggshells often mimic the colour and pattern of host eggs to avoid host detection and parasite chicks are adept at winning the preferential care of host parents, sometimes with specialized adaptations to kill foster siblings outright [15].

Among non-avian vertebrates, brood parasitism is known only from a single fish [16]. Cuckoo catfish (*Synodontis multipunctatus*) take advantage of cichlid hosts that provide care by mouthbrooding developing young. Cuckoo catfish biology remains poorly known, but this issue includes new studies that show the species is tractable for experimental research (see [17,18], this issue). Why is brood parasitism not known from the many other vertebrate clades that provide costly parental care, such as mammals, amphibians and reptiles? We might speculate that viviparity and extended gestation greatly limit opportunities for inserting foreign young into another's brood, and for deceiving carers that another species is kin. But this does not satisfactorily explain why, for example, care-giving frogs or crocodilians (birds' closest reptilian relatives) seem not to experience brood parasitism [19–21]. It is tempting to wonder whether examples may exist that have yet to be detected.

The other major taxonomic group where hosts are co-opted into raising offspring of other species is the insects (reviewed in [22,23] in this issue). Brood-parasitic insects include some beetles, butterflies, true bugs and both social and solitary-living hymenoptera (ants, bees and wasps). Brood parasitism in insects is typically defined by whether the parasite exploits resources acquired by solitary parents ('brood parasites', or 'kleptoparasites'), or by societies that care collectively for their young ('social parasites') (see [23], this issue, for

discussion). In the latter case, the brood parasite often remains in the host nest and uses the host's workers to provision her offspring. For example, in the obligate slave-making ant *Polyergus breviceps*, the invading queen kills off the resident host queen and uses chemical manipulation to ensure that the host workers care for her brood of future queens and males. Female 'kleptoparasites', by contrast, tend to lay their egg/s and leave. For example, cuckoo wasps (Chrysidinae) parasitize solitary bee and wasp species by laying their eggs in the host's nest chamber, such that the parasitic larvae consume the stored resources that had been intended for the host brood, and sometimes also the host egg itself. In this special issue, we take an inclusive approach and define interspecific brood parasitism as any case in which one species usurps the resources intended for parental care by another species, regardless of whether the costs are borne by host parents or cooperative groups (or indeed, the brood; see Cotter *et al.* [24] in this issue), or whether the adult brood parasite leaves or remains in the host nest. Brood parasitism can also occur within a species, where one female exploits the efforts of a conspecific [25], or it can be facultative across species; however, the research in this special issue focuses on obligate parasites, because these have the most potential to influence the evolution of another species.

There has thus been long-standing interest in brood parasitism, both as a fascinating natural history phenomenon and as a window into coevolution. Yet, there is still a great deal that is unknown about when, why and how brood parasitism evolves, and the extent to which it drives evolution in host species. In particular, we lack a comprehensive understanding of how ecology and evolutionary history constrain or facilitate these adaptations, via the mechanisms that shape or respond to selection. This special issue aims to illustrate the diverse ways in which current research is addressing gaps in our knowledge of brood parasitism, to bring together examples of interspecific brood parasitism from across the animal kingdom and to consider how research on brood parasitism may benefit from, and in turn perhaps help to inform, related topics such as social evolution and immunity.

2. Taxonomic boundaries to brood parasitism research

An understanding of brood parasitism in any one system often requires study of system-specific traits, which can obscure general insights across taxa. For example, avian brood parasites manipulate their hosts primarily in the visual or auditory sensory domains (so far as is known), while insect brood parasites must subvert predominantly chemical communication systems to usurp host resources (but see [26] for an example of acoustic mimicry in ants). This difference is at least partly responsible for a tendency towards different types of research programmes in the two taxonomic groups. The visual and acoustic signals of avian parasites are amenable to manipulation in the field, such that much research has focused on understanding how parasites deceive. Evidence of this lies in the many field experiments that add model eggs to nests, or use vocal playbacks of nestlings begging, to understand host responses to alien eggs and chicks (e.g. [27–29]). Chemical signals in insects are less readily manipulated in this way, and insect nests are often less accessible *in situ*. Much research into the brood parasitism of insect societies also focuses on defence mechanisms of hosts and counter-adaptations of the brood parasite. Yet
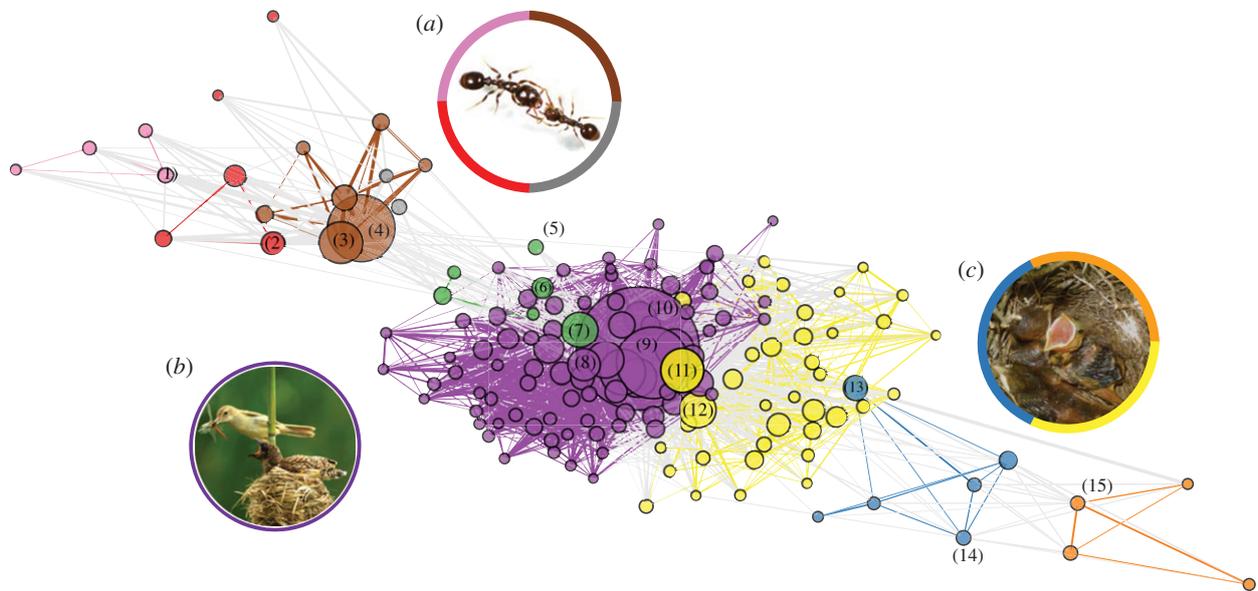
'Insects': (1) Bourke 1991 [37], (2) Buschinger 1986 [38], (3) Wilson 1971 [39], (4) Hölldobler 1990 [40]; 'Coevolution': (5) Darwin 1859 [41], (6) Kilner 2011 [31], (7) Dawkins 1979 [4]; 'Cuckoos': (8) Davies 1989 [42], (9) Rothstein 1990 [43], (10) Davies 2000 [6]; 'Cowbirds': (11) Rothstein 1975 [44], (12) Friedmann 1929 [45], (13) Burnham 2002 [46], (14) Brittingham 1983 [47], (15) Robinson 1995 [48]

Figure 1. Co-citation network of brood parasitism publications. The top 10% of co-cited documents from a *Scopus* search are plotted using a Fruchterman layout; nodes represent co-cited documents (scaled by betweenness centrality) with key publications labelled (first author and year published given below, all plotted publications listed in Supplementary Table 1), and edges represent co-citations (thickness indicates frequency, only edges > 5 are plotted). Node and edge colour represent communities assigned by a walktrap clustering algorithm, and pale grey edges represent links among these communities. Inset photos show the main taxa associated with the coloured co-citation communities: (*a*) host *Temnothorax longispinosus* (right) defends nest from slave-maker *T. americanus* (left) (S. Foitzik); (*b*) Eurasian reed warbler, *Acrocephalus scirpaceus*, feeds a common cuckoo *Cuculus canorus* chick (W. LiQiang/Shutterstock); (*c*) Shiny cowbird *Molothrus bonariensis* begs in the nest with chalk-browed mockingbird *Mimus saturninus* host nest-mates (R. Gloag). The green community to the left represents coevolutionary theory and integrative reviews.

these questions are naturally addressed in the context of social living and indirect fitness (e.g. [22,23,30] in this issue); questions that are rarely considered in avian systems ([31] and [30] in this issue).

To visualize how these and other differences affect the cross-pollination of ideas and theory across taxonomic boundaries (e.g. [32]), we used the bibliometrix package [33] in R (version 3.5.2 [34]) to construct a co-citation network [35,36]. Looking simply at which papers are cited most often, or cited by other papers within a search-set, can give an idea of how connected a research topic is, but it is less effective at identifying how sub-topics are connected. Co-citation networks, on the other hand, are built by measuring which publications are cited together by the papers within a search-set. The more that papers are cited together, the more likely they represent key ideas or concepts of a research topic (or sub-topic) [35,36]. First, we searched *Scopus* for all journal articles published with 'brood parasitism' or 'social parasitism' in the title, abstract or keywords. We focused on obligate parasitism, and therefore excluded papers using 'intraspecific' or 'conspecific' as search terms. We also excluded journals unrelated to biology. Of 1933 articles meeting these criteria, 45.7% (883) included 'bird', 'aves' or 'avian' in the title, abstract or keywords, and 33.6% (650) included 'insect', 'hymenopt*', 'lepidopt*', 'coleopt*', 'beetle', 'butterfly', 'ant', 'wasp' or 'bee'. It is likely that this simple search did not capture all papers published on brood parasitism, as the use of taxonomic keywords can be inconsistent. Nevertheless, we chose not to bias the search by including 'cuckoo' or 'inquiline', for example, as search terms. We next used these two taxonomic groupings of papers ($n = 1533$) to

be confident that we were capturing appropriate papers to build the co-citation network. Here, we plot the top 10% of articles that were cited most commonly with others for visual clarity (figure 1). As expected, we can see clear subfields of brood parasitism research that largely align with taxonomic groupings identified by assigning each publication to the main taxa it described (figure 1). Where co-citation occurred between subfields (grey lines in figure 1), these involved a handful of review papers comparing insects and birds (e.g. [31,49]), reviews of the well-studied common cuckoo [6,50] or early work on arms races and coevolution [4,51].

3. Integrating brood parasitism research

Taking an integrative approach to address key questions in biology is not new, but it is currently experiencing a renaissance [52–54]. In part, this is because addressing questions from multiple perspectives should provide a more comprehensive understanding of what can, and cannot, evolve [53,55]. As well as asking both proximate and ultimate questions about the same suite of traits, different taxa can also provide different windows into the same strategy. Despite the obvious life-history differences, there are many points of comparison between brood parasitism in different systems, and comparative work has a rich potential to identify general principles. For example, Kilner & Langmore's 2011 review [31] integrating coevolutionary studies of brood-parasitic birds and insects was able to derive general hypotheses about why host defences differ so markedly across both taxa. They proposed that the

relative balance of strategy facilitation (whereby one form of defence promotes another) and strategy blocking (whereby one form of defence relaxes selection on an another) may explain this diversity, and predicted which general ecological conditions should drive different coevolutionary trajectories in both birds and insects. Nevertheless, these ideas remain untested; we hope this special issue will increase researcher dialogue across taxonomic boundaries. We have brought together research and reviews on brood parasitism in birds, insects and fish that address complementary questions. These studies cover three key themes that are common to brood parasitism, regardless of the study system.

(a) Adaptations for (and against) deception

All brood parasites must deceive their host to successfully usurp resources, either by avoiding detection during nest invasion (e.g. both common cuckoos and cuckoo wasps time parasitism events for when hosts are less likely to be active at the nest, see [24], this issue) or by avoiding recognition if detected (e.g. many insect brood parasites rely on acquiring chemical signatures of their hosts to reduce aggression; see reviews in this issue [22–24]). Understanding which adaptations arise requires knowledge of reciprocal adaptations in host defence, as these alter and determine the strength of selection acting on brood parasites (e.g. cuckoo finch *Anomalospiza imberbis* hosts appear sensitive to higher-level pattern features of alien eggs, implying that selection acts on parasites to mimic these, see [56] in this issue). Similarly, elucidating the mechanisms that underpin such adaptations is critical, as these can constrain the direction of evolutionary pathways of both parasite (see contributions by Litman [23] and Cotter *et al.* [24] in this issue) and host (see Yang *et al.* [57] and Spottiswoode & Busch [58] in this issue). New technologies and modelling approaches have led to a recent surge in research in the mechanisms underlying brood-parasite and host coevolution, such as sensory systems, cognition, development and genetics. In this special issue, these advances are highlighted by Kaur *et al.* [59], who demonstrate how studies of gene expression can provide clues as to how parasites manipulate host defence, while Stoddard *et al.* [56] apply new mathematical models of pattern matching to reveal new depth in egg recognition by avian hosts, and Hanley *et al.* [60] use visual modelling to show surprising sensory biases in whether hosts decide to reject a foreign egg. This new wave of mechanistic research has enabled a step-change in our understanding of how parasite and host adaptations coevolve.

(b) Diversity and predictability of coevolution

Coevolution between brood parasites and hosts occurs across a variety of degrees of phylogenetic distance; a parasite and its host can come from either a different order (e.g. birds: cuculiform cuckoos versus passeriform hosts, insects: *Maculinea* butterflies versus *Myrmica* ant hosts), a different family (e.g. birds: icterid cowbirds versus parulid warbler hosts, insects: cuckoo wasps targeting solitary bees) or different genera within the same family (e.g. *Vidua* finches versus estrildid finch hosts; inquiline ants that parasitize sister species [22,61]). Brood parasitism is also diverse in its degree of specialism, with some parasites specializing on a single host species (as in *Vidua* finches, and many inquilines), and others (such as the brown-headed cowbird *Molothrus ater*, and *Maculinea* butterflies) using multiple host species. There is often also

variation within generalist species across a parasite's range, such that a host species is heavily parasitized in one locale, but little or never targeted in another, setting the ecological stage for possible geographical mosaics of coevolution that may help to explain otherwise puzzling variation in coevolutionary sophistication [62]. Insights into predictability of brood-parasitic systems may then be gained by comparing the different evolutionary routes by which parasites arise from non-parasitic ancestors across taxonomic groups, the extent to which parasites and hosts vary ecologically across populations and how divergent coevolution among such populations may drive diversification [49]. Research at the coevolutionary interface between ecology and evolution is becoming more important as environments change (e.g. [63]). In this issue, for example, Suhonen *et al.* [64] use a comparative approach to identify bumblebees, ants and wasps that may play host to brood parasites, many of which are species of conservation concern. Tartally *et al.* [65] examine the spatial mosaic in host use across Europe by brood-parasitic *Maculinea* butterflies, and shed light on the role of host switches and local extinctions in the regional persistence of this spectacular genus.

(c) Windows into social evolution

Brood parasitism in any taxonomic group is a derived behaviour of parental care. Therefore, understanding how cheating by brood parasites evolves requires knowledge of the costs and benefits of providing parental care (see [24], this issue), and who pays these costs (see [30], this issue). Any social behaviour is vulnerable to a cheater phenotype, and answering the question of what keeps costly social behaviours, especially social cooperation, evolutionarily stable is of broad relevance in biology. Can brood parasitism provide insight into the evolution of other life-history strategies? In this special issue, Cini *et al.* [22] consider this for sociality, Gloag & Beekman [30] for inclusive fitness and Riehl & Feeney [14] for cooperative breeding. These studies focus on the brood parasites of social insects and/or birds, but brood-parasitic cuckoo catfish may provide new avenues for similar work if we can experimentally modify the amount of care, or paternity certainty, of cichlid host males (a point argued by Polacik *et al.* [17] in this issue). In the final paper of this special issue, Cotter *et al.* [24] use the concept of host defences as a social good to ask whether viewing brood parasitism through the lens of social immunity can help to inform our understanding of social defences.

4. Tinbergen's 'cuckoos'

Over 50 years ago, Tinbergen [66] published his landmark paper that provided a framework for integrative studies into behaviour. Here, he suggested that to fully comprehend how and why a trait evolves, we must address 'Four questions' regarding: (i) the mechanisms that facilitate the trait, (ii) the developmental environment that alters expression of the trait, (iii) the fitness consequences of a trait, and (iv) the similarities and differences of the trait across a phylogeny (also see [67]). Arguably, research into brood-parasite evolution has focused mostly on fitness consequences (that is, 'Question Three'), a bias that is not unusual in the study of animal behaviour ([53,68]). This has led to great advances in our understanding of the requisite adaptations of brood parasites and counter-adaptations for host defences (e.g. birds [8], ants [69], bees [70], wasps [71]). Comparatively less attention has been given

Table 1. Contributions to this special issue according to Tinbergen's Four Questions framework [54] for integrative studies (summaries of each question from [55]) and examples of broad questions in each category that inform our understanding of the coevolutionary biology of brood parasitism. Note that several contributions address more than one question and so appear more than once in the table.

'4 Questions'	Special issue contributions	Example research questions:
(1) Mechanism "How does it work?"	Stoddard et al. [56]	What cognitive rules do hosts use to distinguish kin from non-kin?
	Yang et al. [57]	**What molecular mechanisms underpin parasite adaptations?**
	Kaur et al. [59]	How are host defences constrained by sensory mechanisms?
	Hanley et al. [60]	
	McClelland et al. [76]	
(2) Development "How does it develop?"	Cohen et al. [18]	Does rearing environment influence plasticity of defences?
	Kaur et al. [59]	**Do parasites learn to recognise suitable hosts during development via imprinting?**
	McClelland et al. [76]	How do brood parasites overcome developmental constraints?
(3) Function "What is it for?"	Polacik et al. [17]	What adaptations are necessary for parasites to succeed?
	Litman [23]	**How do parasites differ in morphology, behaviour and physiology to non-parasites?**
	Yang et al. [57]	
	Spottiswoode & Busch [58]	Why do counter-adaptations used by hosts to defend against parasites vary?
	Kaur et al. [59]	**Does hosting a brood parasite affect life-time reproductive success?**
	Tartally et al. [65]	
	Medina & Langmore [77]	
(4) Evolution "How did it evolve?"	Riehl & Feeney [14]	How readily can parasites switch hosts?
	Cohen et al. [18]	**Are the outcomes of coevolutionary arms' races predictable?**
	Cini et al. [22]	Can inclusive fitness theory predict the evolution of parasitism?
	Gloag & Beekman [30]	**What are the evolutionary origins of brood parasitism?**
	Cotter et al. [24]	
	Suhonen et al. [64]	
	McClelland et al. [76]	
	Medina & Langmore [77]	

to understanding these adaptations from a mechanistic viewpoint, the role of the developmental environment in shaping adaptations, or how they vary across species and time, although recent research trends suggest this is changing. Questions of development in particular are becoming ever more timely, alongside our increasing appreciation for the role of phenotypic plasticity and learning in the evolutionary process [72–74], and in the context of the pressing need to understand and predict how populations will respond to rapid environmental change [75]. For brood parasitism research, therefore, the time seems ripe to revisit Tinbergen's proposed framework. The studies and reviews in this special issue all cover one or more of Tinbergen's Four Questions (table 1); for example, McClelland et al. [76] demonstrate how combining analyses of mechanisms across species sheds light on the traits that may make brood-parasitic birds successful; Cohen et al. [18] examine the ontogeny of brood-parasitic catfish and non-parasitic congeners to show that advanced development in this system is not an adaptation for parasitism, as we might expect if we only compared it against its host; and Medina & Langmore [77] link field experiments with evolutionary comparative analyses across hosts of brood-parasitic birds to test how population density influences fitness. We hope this encourages future research that integrates mechanism, development and phylogeny with the fitness consequences of traits to understand brood parasitism evolution.

5. Conclusion

For many of us, brood parasitism is the perfect marriage of natural history and evolutionary biology. Yet, at present, natural history is arguably more limiting to our efforts to understand coevolution than either ideas or methods. This is because the best way to test our current understanding is to validate it in diverse natural systems. In the case of birds, a recent explosion of studies in previously little-known systems has demonstrated this truth, by challenging some long-standing ideas (for example, that chick rejection cannot evolve [78–80]), and supporting others (for example, the role of maternal inheritance in the faithful transmission of parasitic specialization [81–83]). The systems enjoying most new attention are tropical and south-temperate species in Asia, Australasia, Africa and South America, where selection pressures are often quite different from those of the classic avian systems of the northern hemisphere owing in part to longer reproductive lives and opportunities for learning that likely shift the costs and benefits of defensive decisions in any one breeding attempt. New natural history has similar potential in non-avian systems. For example, the past decade has seen the discovery of several

new species of inquilines of Neotropical attine fungus-growing ants [84,85], including one in the process of speciating from its host [86]. These have provided new opportunities to test theories of inquiline evolution [86]. Looking ahead, we hope that adventurous biologists continue to uncover the natural history of the many brood parasites about which tantalizingly little remains known, and perhaps to even discover brood parasitism for the first time in new taxa.

References

1. Clutton-Brock TH. 1991 *The evolution of parental care*. Princeton, NJ: Princeton University Press.
2. Schulze-Hagen K, Stokke BG, Birkhead TR. 2008 Reproductive biology of the European Cuckoo *Cuculus canorus*: early insights, persistent errors and the acquisition of knowledge. *J. Ornithol.* **150**, 1–16. (doi:10.1007/s10336-008-0340-8)
3. Lai C. 1998 Messenger of spring and morality: cuckoo lore in Chinese sources. *J. Am. Orient. Soc.* **118**, 530–542. (doi:10.2307/604785)
4. Dawkins R, Krebs JR. 1979 Arms races between and within species. *Proc. R. Soc. Lond. B* **205**, 489–511. (doi:10.1098/rspb.1979.0081)
5. Thompson JN. 2013 *Relentless evolution*. Chicago, IL: University of Chicago Press.
6. Davies NB. 2000 *Cuckoos, cowbirds and other cheats*. London, UK: Poyser.
7. Klug H, Bonsall MB. 2010 Life history and the evolution of parental care. *Evolution* **64**, 823–835. (doi:10.1111/j.1558-5646.2009.00854.x)
8. Soler M. 2014 Long-term coevolution between avian brood parasites and their hosts. *Biol. Rev.* **89**, 688–704. (doi:10.1111/brv.12075)
9. Feeney WE, Welbergen JA, Langmore NE. 2014 Advances in the study of coevolution between avian brood parasites and their hosts. *Annu. Rev. Ecol. Evol. Syst.* **45**, 227–246. (doi:10.1146/annurev-ecolsys-120213-091603)
10. Soler M. 2017 *Avian brood parasitism: behaviour, ecology, evolution and coevolution*. Berlin, Germany: Springer.
11. Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO. 2012 The global diversity of birds in space and time. *Nature* **491**, 444–448. (doi:10.1038/nature11631)
12. Sorenson MD, Payne RB. 2002 Molecular genetic perspectives on avian brood parasitism. *Integr. Comp. Biol.* **42**, 388–400. (doi:10.1093/icb/42.2.388)
13. Feeney WE, Medina I, Somveille M, Heinsohn R, Hall ML, Mulder RA, Stein JA, Kilner RM, Langmore NE. 2013 Brood parasitism and the evolution of cooperative breeding in birds. *Science* **342**, 1506–1508. (doi:10.1126/science.1240039)
14. Feeney WE, Riehl C. 2019 Monogamy without parental care? Social and genetic mating systems of avian brood parasites. *Phil. Trans. R. Soc. B* **374**, 20180201. (doi:10.1098/rstb.2018.0201)
15. Davies NB. 2011 Cuckoo adaptations: trickery and tuning. *J. Zool.* **284**, 1–14. (doi:10.1111/j.1469-7998.2011.00810.x)
16. Sato T. 1986 A brood parasitic catfish of mouthbrooding cichlid fishes in Lake Tanganyika. *Nature* **323**, 58–59. (doi:10.1038/323058a0)
17. Polačik M, Reichard M, Smith C, Blažek R. 2019 Parasitic cuckoo catfish exploit parental responses to stray offspring. *Phil. Trans. R. Soc. B* **374**, 20180412. (doi:10.1098/rstb.2018.0412)
18. Cohen MS, Hawkins MB, Stock DW, Cruz A. 2019 Early life-history features associated with brood parasitism in the cuckoo catfish, *Synodontis multipunctatus* (Siluriformes: Mochokidae). *Phil. Trans. R. Soc. B* **374**, 20180205. (doi:10.1098/rstb.2018.0205)
19. Crump ML. 1996 Parental care among the amphibia. *Adv. Study Behav.* **25**, 109–144. (doi:10.1016/S0065-3454(08)60331-9)
20. Brown JL, Morales V, Summers K. 2009 Tactical reproductive parasitism via larval cannibalism in Peruvian poison frogs. *Biol. Lett.* **5**, 148–151. (doi:10.1098/rsbl.2008.0591)
21. Gans C. 1996 An overview of parental care among the Reptilia. *Adv. Study Behav.* **25**, 145–160. (doi:10.1016/S0065-3454(08)60332-0)
22. Cini A, Sumner S, Cervo R. 2019 Inquiline social parasites as tools to unlock the secrets of insect sociality. *Phil. Trans. R. Soc. B* **374**, 20180193. (doi:10.1098/rstb.2018.0193)
23. Litman JR. 2019 Under the radar: detection avoidance in brood parasitic bees. *Phil. Trans. R. Soc. B* **374**, 20180196. (doi:10.1098/rstb.2018.0196)
24. Cotter SC, Pincheira-Donoso D, Thorogood R. 2019 Defences against brood parasites from a social immunity perspective. *Phil. Trans. R. Soc. B* **374**, 20180207. (doi:10.1098/rstb.2018.0207)
25. Lyon BE, Eadie JM. 2008 Conspecific brood parasitism in birds: a life-history perspective. *Annu. Rev. Ecol. Evol. Syst.* **39**, 343–363. (doi:10.1146/annurev.ecolsys.39.110707.173354)
26. Barbero F, Thomas JA, Bonelli S, Balletto E, Schönrogge K. 2009 Queen ants make distinctive sounds that are mimicked by a butterfly social parasite. *Science* **323**, 782–785. (doi:10.1126/science.1163583)
27. York JE, Davies NB. 2017 Female cuckoo calls misdirect host defences towards the wrong enemy. *Nat. Ecol. Evol.* **1**, 1520–1525. (doi:10.1038/s41559-017-0279-3)
28. Kilner RM, Noble DG, Davies NB. 1999 Signals of need in parent–offspring communication and their exploitation by the common cuckoo. *Nature* **397**, 667–672. (doi:10.1038/17746)
29. Strausberger BM, Rothstein SI. 2009 Parasitic cowbirds may defeat host defense by causing rejecters to misimprint on cowbird eggs. *Behav. Ecol.* **20**, 691–699. (doi:10.1093/beheco/arp042)
30. Gloag R, Beekman M. 2019 The brood parasite's guide to inclusive fitness theory. *Phil. Trans. R. Soc. B* **374**, 20180198. (doi:10.1098/rstb.2018.0198)
31. Kilner RM, Langmore NE. 2011 Cuckoos versus hosts in insects and birds: adaptations, counter-adaptations and outcomes. *Biol. Rev. Camb. Philos. Soc.* **86**, 836–852. (doi:10.1111/j.1469-185X.2010.00173.x)
32. Youngblood M, Lahti D. 2018 A bibliometric analysis of the interdisciplinary field of cultural evolution. *Palgrave Commun.* **4**, 120. (doi:10.1057/s41599-018-0175-8)
33. Aria M, Cuccurullo C. 2017 bibliometrix: an R-tool for comprehensive science mapping analysis. *J. Informetr.* **11**, 959–975. (doi:10.1016/j.joi.2017.08.007)
34. R Core Team. 2018 *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.
35. Small H. 1973 Co-citation in the scientific literature: a new measure of the relationship between two documents *J. Am. Soc. Inf. Sci.* **24**, 265–269. (doi:10.1002/asi.4630240406)

36. Trujillo CM, Long TM. 2018 Document co-citation analysis to enhance transdisciplinary research. *Sci. Adv.* **4**, e1701130. (doi:10.1126/sciadv.1701130)

37. Bourke AFG, Franks NR. 1991 Alternative adaptations, sympatric speciation and the evolution of parasitic, inquiline ants. *Biol. J. Linn. Soc.* **43**, 157–178. (doi:10.1111/j.1095-8312.1991.tb00591.x)

38. Buschinger A. 1986 Evolution of social parasitism in ants. *Trends Ecol. Evol.* **1**, 155–160. (doi:10.1016/0169-5347(86)90044-3)

39. Wilson EO. 1971 *The insect societies*. Cambridge, MA: Harvard University Press.

40. Hölldobler B, Wilson EO. 1990 *The ants*. Cambridge, MA: Harvard University Press.

41. Darwin CR. 1859 *On the origin of species*. London, UK: John Murray.

42. Davies NB, Brooke M. 1989 An experimental study of co-evolution between the cuckoo, *Cuculus canorus*, and its hosts. II. Host egg markings, chick discrimination and general discussion. *J. Anim. Ecol.* **58**, 225–236. (doi:10.2307/4996)

43. Rothstein SI. 1990 A model system for coevolution: avian brood parasitism. *Annu. Rev. Ecol. Syst.* **21**, 481–508.

44. Rothstein SI. 1975 Evolutionary rates and host defenses against avian brood parasitism. *Am. Nat.* **109**, 161–176. (doi:10.1086/282984)

45. Friedmann H. 1929 *The cowbirds: a study in the biology of social parasitism*. Springfield, IL: CC Thomas.

46. Burnham K, Anderson D. 2002 *Model selection and multimodel inference: a practical information-theoretic approach*. New York, NY: Springer-Verlag.

47. Brittingham MC, Temple SA. 1983 Have cowbirds caused forest songbirds to decline? *Bioscience* **33**, 31–35. (doi:10.2307/1309241)

48. Robinson SK, Thompson FR, Donovan TM, Whitehead DR, Faaborg J. 1995 Regional forest fragmentation and the nesting success of migratory birds. *Science* **267**, 1987–1990. (doi:10.1126/science.267.5206.19878787)

49. Davies NB, Bourke AFG, Brooke M. 1989 Cuckoos and parasitic ants: interspecific brood parasitism as an evolutionary arms race. *Trends Ecol. Evol.* **4**, 274–278. (doi:10.1016/0169-5347(89)90202-4)

50. Wyllie I. 1981 *The cuckoo*. New York, NY: Universe Books.

51. Thompson JN. 1994 *The coevolutionary process*. Chicago, IL: University of Chicago Press.

52. Wake MH. 2003 What is 'integrative biology'? *Integr. Comp. Biol.* **43**, 239–241. (doi:10.1093/icb/43.2.239)

53. Aubin-Horth N. 2016 Using an integrative approach to investigate the evolution of behaviour. *Evol. Appl.* **9**, 166–180. (doi:10.1111/eva.12300)

54. MacDougall-Shackleton SA. 2011 The levels of analysis revisited. *Phil. Trans. R. Soc. B* **366**, 2076–2085. (doi:10.1098/rstb.2010.0363)

55. Stearns SC, Magwene P. 2003 The naturalist in a world of genomics. *Am. Nat.* **161**, 171–180.

56. Stoddard MC, Hogan BG, Stevens M, Spottiswoode CN. 2019 Higher-level pattern features provide additional information to birds when recognizing and rejecting parasitic eggs. *Phil. Trans. R. Soc. B* **374**, 20180197. (doi:10.1098/rstb.2018.0197)

57. Yang C, Liang W, Møller A. 2019 Egg retrieval versus egg rejection in cuckoo hosts. *Phil. Trans. R. Soc. B* **374**, 20180200. (doi:10.1098/rstb.2018.0200)

58. Spottiswoode CN, Busch R. 2019 Vive la difference! Self/non-self recognition and the evolution of signatures of identity in arms races with parasites. *Phil. Trans. R. Soc. B* **374**, 20180206. (doi:10.1098/rstb.2018.0206)

59. Kaur R, Stoldt M, Jongepier E, Feldmeyer B, Menzel F, Bornberg-Bauer E, Foitzik S. 2019 Ant behaviour and brain gene expression of defending hosts depend on the ecological success of the intruding social parasite. *Phil. Trans. R. Soc. B* **374**, 20180192. (doi:10.1098/rstb.2018.0192)

60. Hanley D, López AV, Fiorini VD, Reboreda JC, Grim T, Hauber ME. 2019 Variation in multicomponent recognition cues alters egg rejection decisions: a test of the optimal acceptance threshold hypothesis. *Phil. Trans. R. Soc. B* **374**, 20180195. (doi:10.1098/rstb.2018.0195)

61. Huang MH, Dornhaus A. 2008 A meta-analysis of ant social parasitism: host characteristics of different parasitism types and a test of Emery's rule. *Ecol. Entomol.* **33**, 589–596. (doi:10.1111/j.1365-2311.2008.01005.x)

62. Thompson JN. 2005 *The geographic mosaic of coevolution*. Chicago, IL: University of Chicago Press.

63. Péron G, Altwegg R, Jamie GA, Spottiswoode CN. 2016 Coupled range dynamics of brood parasites and their hosts responding to climate and vegetation changes. *J. Anim. Ecol.* **85**, 1191–1199. (doi:10.1111/1365-2656.12546)

64. Suhonen J, Ilvonen JJ, Nyman T, Sorvari J. 2019 Brood parasitism in eusocial insects (Hymenoptera): role of host geographical range size and phylogeny. *Phil. Trans. R. Soc. B* **374**, 20180203. (doi:10.1098/rstb.2018.0203)

65. Tartally A et al. 2019 Patterns of host use by brood parasitic *Maculinea* butterflies across Europe. *Phil. Trans. R. Soc. B* **374**, 20180202. (doi:10.1098/rstb.2018.0202)

66. Tinbergen N. 1963 On aims and methods of ethology. *Z. Tierpsychol.* **20**, 410–433. (doi:10.1111/j.1439-0310.1963.tb01161.x)

67. Bateson P, Laland KN. 2013 Tinbergen's four questions: an appreciation and an update. *Trends Ecol. Evol.* **28**, 712–718. (doi:10.1016/j.tree.2013.09.013)

68. Bolhuis JJ, Verhulst S. 2009 *Tinbergen's legacy: function and mechanism in behavioral biology*. Cambridge, UK: Cambridge University Press.

69. Buschinger A. 2009 Social parasitism among ants: a review (Hymenoptera: Formicidae). *Myrmecol. News* **12**, 219–235.

70. Cardinal S, Straka J, Danforth BN. 2010 Comprehensive phylogeny of apid bees reveals the evolutionary origins and antiquity of cleptoparasitism. *Proc. Natl Acad. Sci. USA* **107**, 16 207–16 211. (doi:10.1073/pnas.1006299107)

71. Cervo R. 2006 Polistes wasps and their social parasites: an overview. *Ann. Zool. Fennici* **43**, 531–549. (doi:10.2307/23736760)

72. West-Eberhard MJ. 2003 *Developmental plasticity and evolution*. Oxford, UK: Oxford University Press.

73. Mason PA. 2016 On the role of host phenotypic plasticity in host shifting by parasites. *Ecol. Lett.* **19**, 121–132. (doi:10.1111/ele.12555)

74. Whiten A. 2017 A second inheritance system: the extension of biology through culture. *Interface Focus* **7**, 20160142. (doi:10.1098/rsfs.2016.0142)

75. Sih A, Ferrari MCO, Harris DJ. 2011 Evolution and behavioural responses to human-induced rapid environmental change. *Evol. Appl.* **4**, 367–387. (doi:10.1111/j.1752-4571.2010.00166.x)

76. McClelland SC, Jamie GA, Waters K, Caldas L, Spottiswoode CN, Portugal SJ. 2019 Convergent evolution of reduced eggshell conductance in avian brood parasites. *Phil. Trans. R. Soc. B* **374**, 20180194. (doi:10.1098/rstb.2018.0194)

77. Medina I, Langmore NE. 2019 Host density predicts the probability of parasitism by avian brood parasites. *Phil. Trans. R. Soc. B* **374**, 20180204. (doi:10.1098/rstb.2018.0204)

78. Lotem A. 1993 Learning to recognize nestlings is maladaptive for cuckoo *Cuculus canorus* hosts. *Nature* **362**, 743–745. (doi:10.1038/362743a0)

79. Langmore NE, Hunt S, Kilner RM. 2003 Escalation of a coevolutionary arms race through host rejection of brood parasitic young. *Nature* **422**, 157–160. (doi:10.1038/nature01460)

80. Sato NJ, Tokue K, Noske RA, Mikami OK, Ueda K. 2010 Evicting cuckoo nestlings from the nest: a new anti-parasitism behaviour. *Biol. Lett.* **6**, 67–69. (doi:10.1098/rsbl.2009.0540)

81. Punnett RC. 1933 Inheritance of egg-colour in the 'parasitic' cuckoos. *Nature* **132**, 892–893. (doi:10.1080/0300443032000088212)

82. Spottiswoode CN, Stryjewski KF, Quader S, Colebrook-Robjent JFR, Sorenson MD. 2011 Ancient host specificity within a single species of brood parasitic bird. *Proc. Natl Acad. Sci. USA* **108**, 17 738–17 742. (doi:10.1073/pnas.1109630108)

83. Fossøy F et al. 2016 Ancient origin and maternal inheritance of blue cuckoo eggs. *Nat. Commun.* **7**, 10272. (doi:10.1038/ncomms10272)

84. Rabeling C, Bacci Jr M. 2010 A new workerless inquiline in the Lower Attini (Hymenoptera: Formicidae), with a discussion of social parasitism in fungus-growing ants. *Syst. Entomol.* **35**, 379–392. (doi:10.1111/j.1365-3113.2010.00533.x)

85. De Souza DJ, Soares IMF, Della Lucia TMC. 2007 *Acromyrmex ameliae* sp. n. (Hymenoptera: Formicidae): a new social parasite of leaf-cutting ants in Brazil. *Insect Sci.* **14**, 251–257. (doi:10.1111/j.1744-7917.2007.00151.x)

86. Rabeling C, Schultz TR, Pierce NE, Bacci M. 2014 A social parasite evolved reproductive isolation from its fungus-growing ant host in sympatry. *Curr. Biol.* **24**, 2047–2052. (doi:10.1016/j.cub.2014.07.048)