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Introduction

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The coevolutionary biology of brood parasitism: a call for integration

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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].

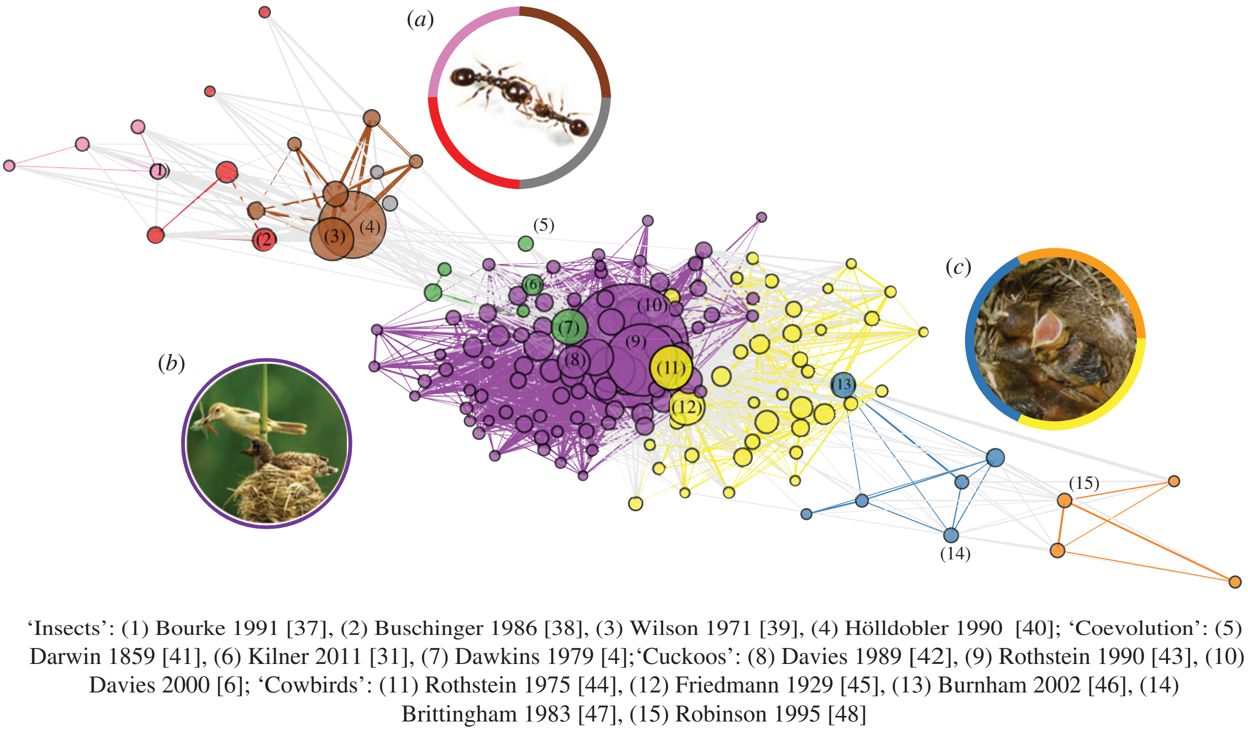
Among non-avian vertebrates, brood parasitism is known only from a single fish [16]. Cuckoo catfish (*Synodontis multipunctatus*) take advantage of cichlid hosts that provide care by mouthbrooding developing young. Cuckoo catfish biology remains poorly known, but this issue includes new studies that 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	Stoddard *et al.* [56]	*What cognitive rules do hosts use to distinguish kin from non-kin?*
"How does it work?"	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	Cohen *et al.* [18]	*Does rearing environment influence plasticity of defences?*
"How does it develop?"	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	Polacik *et al.* [17]	*What adaptations are necessary for parasites to succeed?*
"What is it for?"	Litman [23]	***How do parasites differ in morphology, behaviour and physiology to non-parasites?***
	Yang *et al.* [57]	*Why do counter-adaptations used by hosts to defend against parasites vary?*
	Spottiswoode & Busch [58]	***Does hosting a brood parasite affect life-time reproductive success?***
	Kaur *et al.* [59]	
	Tartally *et al.* [65]	
	Medina & Langmore [77]	
(4) Evolution	Riehl & Feeney [14]	*How readily can parasites switch hosts?*
"How did it evolve?"	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.

Data accessibility. Search results used for the bibliometric analysis are available in the electronic supplementary material.

Authors' contributions. R.T. conceived and carried out the bibliometric analysis; all authors wrote the manuscript.

Competing interests. We have no competing interests.

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