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The coevolutionary biology of brood parasitism: a call for integration

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RT conceived and carried out the bibliometric analysis; all authors wrote the manuscript.

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1 TITLE: **The coevolutionary biology of brood parasitism: a call for**
2 **integration**

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16 ABSTRACT

17 Obligate brood parasitic cheats have fascinated natural historians since ancient times. Passing on the
18 costs of parental care to others occurs widely in birds, insects, and fish, and often exerts selection
19 pressure on hosts which in turn evolve defences. Brood parasites have therefore provided an
20 illuminating system for researching coevolution. Nevertheless, we lack a comprehensive
21 understanding of how ecology and evolutionary history constrain or facilitate these adaptations, via
22 the mechanisms that shape or respond to selection. In this special issue we bring together examples
23 from across the animal kingdom to illustrate the diverse ways in which recent research is addressing
24 this gap. This special issue also considers how research on brood parasitism may benefit from, and in
25 turn inform, related fields such as social evolution and immunity. Here we summarise the taxonomic
26 boundaries that have so far led to disparate understanding of the mechanisms, ontogeny, function
27 and phylogeny of brood parasitism. We suggest that to fully understand coevolution between brood
28 parasites and their hosts we now require a synthesis of these questions across taxa, coupled with
29 renewed vigour in uncovering the natural history of the majority of the world's brood parasites that
30 remain little-known, and in some cases perhaps unknown. Without this we will continue to struggle
31 to address perhaps the most puzzling question about brood parasitism – if parental care is costly, why
32 is brood parasitism not more common?

33 This article is part of the theme issue 'The co-evolutionary biology of brood parasitism: from
34 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 chick (such as a cuckoo, cowbird or honeyguide) 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 6th 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]), 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 (Krebs & Dawkins 1979): 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].

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.

Where do we find brood parasites in nature? Parental care strategies evolve when the fitness benefits to parents of caring for their young outweigh their 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.

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5 72 Parental care is particularly prevalent in birds, and avian brood parasitism has received the
6
7 73 lion's share of research effort into brood parasites (for reviews, see [6,8–10]). Obligate interspecific
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9 74 brood parasitism is found in ~1% of all birds, has evolved independently seven times, and can be found
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11 75 on every continent except Antarctica [6]. Evolutionary transitions to brood parasitism in birds vary
12
13 76 from very ancient (e.g. ~26 million years ago in *Indicator* honeyguides, [11]) to an order of magnitude
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15 77 more recent (e.g. the black-headed duck *Heteronetta atricapilla*, *Molothrus* cowbirds [12]). Typically,
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17 78 avian brood parasites lay their eggs in the nests of host species to take advantage of both incubation
18
19 79 and chick-rearing behaviour. They may exploit the behaviour of a single pair of hosts (parents) or of a
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21 80 unit of cooperatively breeding hosts (parents plus helpers) (e.g.[13], and see [14] in this issue).
22
23 81 Parasites have a suite of adaptations across the life stages that allow successful exploitation of hosts:
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25 82 adult females track the nesting progress of hosts and lay eggs at the appropriate time and place to
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27 83 ensure optimal development, eggshells often mimic the colour and pattern of host eggs to avoid host
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29 84 detection, and parasite chicks are adept at winning the preferential care of host parents, sometimes
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31 85 with specialised adaptations to kill foster siblings outright [15].
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35 87 Among non-avian vertebrates, brood parasitism is known only from a single fish [16]. Cuckoo
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37 88 catfish (*Synodontis multipunctatus*) take advantage of cichlid hosts that provide care by mouth-
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39 89 brooding developing young. Cuckoo catfish biology remains poorly known, but this issue includes a
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41 90 review of recent advances that are making the species more tractable for experimental research (see
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43 91 [17,18], this issue). Why is brood parasitism not known from the many other vertebrate clades that
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45 92 provide costly parental care, such as mammals, amphibians and reptiles? We might speculate that
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47 93 viviparity and extended gestation greatly limits opportunities for inserting foreign young into
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49 94 another's brood, and for deceiving carers that another species is kin. But this does not satisfactorily
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51 95 explain why, for example, care-giving frogs or crocodylians (birds' closest reptilian relatives) seem not
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53 96 to experience brood parasitism [19–21]. It is tempting to wonder whether examples may exist that
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55 97 have yet to be detected.
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59 99 The other major taxonomic group where hosts are co-opted into raising offspring of other
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100 species, are the insects (reviewed by [22,23] in this issue). Brood-parasitic insects include some
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102 beetles, butterflies, true bugs, and both social and solitary-living hymenoptera (ants, bees and wasps).
103
104 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

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3 105 often remains in the host nest and uses the host's workers to provision her sexual offspring. For
4 106 example, in the obligate slave-making ant *Polyergus breviceps*, the invading queen kills off the resident
5 107 host queen and uses chemical manipulation to ensure that the host workers care for her brood of
6 108 future queens and males. Female 'kleptoparasites', by contrast, tend to lay their egg/s and leave. For
7 109 example, cuckoo wasps (Chrysidinae) parasitise solitary bee and wasp species by laying their eggs in
8 110 the host's nest chamber, such that the parasitic larvae consume the stored resources that had been
9 111 intended for the host brood, and sometimes also the host egg itself. While at first glance the
10 112 kleptoparasites may appear more similar to avian brood parasites than the social parasites, similar
11 113 variation in who pays the costs of parasitism also exists in avian systems: brood parasites take
12 114 advantage of monogamous pairs, polygynous nests, and cooperative groups. Therefore in this special
13 115 issue we have chosen to take an inclusive approach and define interspecific brood parasitism as any
14 116 case in which one species usurps the resources intended for parental care by another species.
15 117 Facultative brood parasitism can also occur, of course, within a species, where one female exploits
16 118 the efforts of a conspecific [24], but the research in this special issue focuses on obligate parasites,
17 119 which have the potential to influence the evolution of another species.

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121 **2. TAXONOMIC BOUNDARIES TO BROOD PARASITISM RESEARCH**

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123 An understanding of brood parasitism in any one system often requires study of system-specific traits.
124 For example, avian brood parasites manipulate their hosts primarily in the visual or auditory sensory
125 domains (so far as is known), while insect brood parasites must subvert predominantly chemical
126 communication systems to usurp host resources (but see [25] for an example of acoustic mimicry in
127 ants). This difference generates practical differences in how brood parasitism is studied in the two
128 taxonomic groups. The visual and acoustic signals of avian parasites are fairly amenable to
129 manipulation in the field, as evidenced by the many variations of experiments with model eggs, or
130 playback manipulations at nests, used to investigate host responses to cuckoo eggs and chicks [e.g.
131 [26–28]]. Chemical signals in insects are less readily manipulated in this way, and insect nests are often
132 less accessible *in situ*. Furthermore, research into the social parasitism of insect societies often focuses
133 on questions specific to social living, that do not apply to many avian systems ([29] and [22,23,30] in
134 this issue).

135

136 To visualise how these and other differences affect the cross-pollination of ideas and theory
137 across taxonomic boundaries, we used the bibliometrix package [31] in R (version 3.5.2, [32]) to
138 construct a co-citation network [33]. This approach moves beyond looking at which papers are cited

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3 139 most and instead identifies the key publications that define or link fields; papers cited together most
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5 140 often are more central to the network. First, we searched *Scopus* for all journal articles published with
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7 141 “brood parasitism” or “social parasitism” in the title, abstract, or keywords. We focused on obligate
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9 142 parasitism, and therefore excluded papers using “intraspecific” or “conspecific” as search terms. We
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11 143 also excluded journals unrelated to biology. Of 1933 articles meeting these criteria, 45.7% (883)
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13 144 included “bird”, “aves”, or “avian” in the title, abstract, or keywords, and 33.6% (650) included
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15 145 “insect”, “hymenopt*”, “lepidopt*”, “coleopt*”, “beetle”, “butterfly”, “ant”, “wasp”, or “bee”. It is
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17 146 likely that this simple search did not capture all papers published on brood parasitism, as the use of
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19 147 taxonomic keywords can be inconsistent. Nevertheless, we chose not to bias the search by including
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21 148 “cuckoo” as a search term. We then used these two taxonomic groupings of papers (n = 1533) to be
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23 149 confident that we were capturing appropriate papers to build the co-citation network. Here we plot
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25 150 the top 10% of articles that were cited most commonly with others for visual clarity (Fig.1). As
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27 151 expected, we can see clear subfields of brood parasitism research that largely align with taxonomic
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29 152 groupings (Fig. 1). Where co-citation occurred between subfields (grey lines in Fig. 1), these involved
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31 153 a handful of review papers comparing insects and birds (e.g.[29,34]), reviews of the well-studied
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33 154 common cuckoo [6,35], or early work on arms races and coevolution [4,36].

30 155

31 156 INSERT FIGURE 1 HERE

32 157

36 158 **3. INTEGRATING BROOD PARASITISM RESEARCH**

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38 160 Taking an integrative approach to address key questions in biology is not new, but it is currently
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40 161 experiencing a renaissance [37–39]. In part this is because addressing questions from multiple
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42 162 perspectives should provide a more comprehensive understanding of what can, and cannot, evolve
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44 163 [38,40]. As well as asking both proximate and ultimate questions about the same suite of traits,
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46 164 different taxa can also provide different windows into the same strategy. Despite the obvious life-
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48 165 history differences, there are many points of comparison between brood parasitism in different
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50 166 systems, and comparative work has a rich potential to identify general principles. For example, Kilner
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52 167 & Langmore’s 2011 review [29] integrating coevolutionary studies of brood-parasitic birds and insects
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54 168 was able to derive general hypotheses about why host defences differ so markedly across both taxa.
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56 169 They proposed that the relative balance of strategy-facilitation (whereby one form of defence
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58 170 promotes another) and strategy-blocking (whereby one form of defence relaxes selection on an
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60 171 another) may explain this diversity, and predicted which general ecological conditions should drive
172 different coevolutionary trajectories in both birds and insects. Inspired by such progress, we hope this

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3 173 special issue will increase researcher dialogue across taxonomic boundaries. We have brought
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5 174 together research and reviews on brood parasitism in birds, insects and fish that address
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7 175 complementary questions. These studies cover three key themes that are common to brood
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9 176 parasitism, regardless of the study system:

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13 178 **(a) Adaptations for (and against) deception**

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15 180 All brood parasites must deceive their host to successfully usurp resources, either by avoiding
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17 181 detection during nest invasion (e.g. both common cuckoos and cuckoo wasps time parasitism events
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19 182 for when hosts are less likely to be active at the nest, see [41] this issue), or by avoiding recognition if
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21 183 detected (e.g. many insect brood parasites rely on acquiring chemical signatures of their hosts to
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23 184 reduce aggression; see reviews in this issue by [22,23,41]). Understanding which adaptations arise
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25 185 requires knowledge of reciprocal adaptations in host defence, as these alter and determine the
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27 186 strength of selection acting on brood parasites (e.g. cuckoo finch *Anomalospiza imberbis* hosts appear
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29 187 sensitive to higher-level pattern features of alien eggs, implying that selection acts on parasites to
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31 188 mimic these, see [42] in this issue). Similarly, elucidating the mechanisms that underpin such
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33 189 adaptations is critical, as these can constrain the direction of evolutionary pathways of both parasite
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35 190 (see contributions by Litman [23] and Cotter *et al.* [41] in this issue) and host (see Liang *et al.* [43] and
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37 191 Spottiswoode & Busch [44] in this issue). New technologies and modeling approaches have led to a
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39 192 recent surge in research in the mechanisms underlying brood-parasite and host coevolution, such as
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41 193 sensory systems, cognition, development and genetics. In this special issue, these advances are
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43 194 highlighted by Foitzik *et al.* [45] which demonstrates how studies of gene expression can provide clues
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45 195 as to how parasite's manipulate host defence, while Stoddard *et al.* [42] applies new mathematical
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47 196 models of pattern matching to reveal new depth in egg recognition by avian hosts, and Hanley *et al.*
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49 197 [46] use visual modelling to show surprising sensory biases in whether hosts decide to reject a foreign
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51 198 egg. This new wave of mechanistic research has enabled a step-change in our understanding of how
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53 199 parasite and host adaptations evolve.

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52 201 **(b) Diversity and predictability of coevolution**

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54 203 Coevolution between brood parasites and hosts occurs across a variety of degrees of phylogenetic
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56 204 distance; a parasite and its host can come from either a different order (e.g. birds: cuculiform cuckoos
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58 205 vs. passeriform hosts, insects: *Maculinea* butterflies vs. *Myrmica* ant hosts), a different family (e.g.
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60 206 birds: icterid cowbirds vs. parulid warbler hosts, insects: cuckoo wasps targeting solitary bees), or

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3 207 different genera within the same family (e.g. *Vidua* finches vs. estrildid finch hosts; inquiline ants that
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5 208 parasitise sister species, [22,47]). Brood parasitism is also diverse in its degree of specialism, with
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7 209 some parasites specializing on a single host species (as in *Vidua* finches, and many lycaenid
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9 210 butterflies), and others (such as the brown-headed cowbird *Molothrus ater*, and *Maculinea*
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11 211 butterflies) using hundreds of different host species. There is often also variation within generalist
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13 212 species across a parasite's range, such that a host species is heavily parasitized in one locale, but little
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15 213 or never targeted in another, setting the ecological stage for possible geographical mosaics of
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17 214 coevolution that may help to explain otherwise puzzling variation in coevolutionary sophistication
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19 215 [48]. Insights into the ecological and evolutionary predictability of brood-parasitic systems may then
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21 216 be gained by comparing the different evolutionary routes by which parasites arise from non-parasitic
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23 217 ancestors across taxonomic groups, the extent to which parasites and hosts vary ecologically across
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25 218 populations, and how divergent coevolution among such populations may drive diversification [34].
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27 219 Research at the coevolutionary interface between ecology and evolution is becoming more important
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29 220 as environments change (e.g. [49]). In this issue, for example, Suhonen *et al.* [50] use a comparative
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31 221 approach to identify bumblebees, ants and wasps that may play hosts to brood parasites, many of
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33 222 which are species of conservation concern. Nash *et al.* [51] examine the spatial mosaic in host use
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35 223 across Europe by brood-parasitic *Maculinea* butterflies, and shed light on the role of host switches
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37 224 and local extinctions in the regional persistence of this spectacular genus.
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36 226 **(c) Windows into social evolution**

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39 228 Brood parasitism in any taxonomic group is a derived behaviour of parental care. Therefore,
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41 229 understanding how cheating by brood parasites evolves requires knowledge of the costs and benefits
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43 230 of providing parental care (see [41], this issue), and who pays these costs (see [30], this issue). Any
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45 231 social behaviour is vulnerable to a cheater phenotype, and answering the question of what keeps
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47 232 costly social behaviours, especially social co-operation, evolutionarily stable is a question of broad
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49 233 relevance in biology. Can brood parasitism provide insight into the evolution of other life-history
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51 234 strategies? In this special issue, Cini *et al.* [22] consider this for sociality, Gloag & Beekman [30] for
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53 235 inclusive fitness, and Riehl & Feeney [14] for co-operative breeding. Social insects are perhaps the best
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55 236 system for addressing this question regarding inclusive fitness (e.g. [22,30] in this issue, but see [14]
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57 237 for an example in birds), but if we can experimentally modify the amount of care, or paternity
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59 238 certainty, of cichlid host males, then brood-parasitic cuckoo catfish may provide new avenues (see the
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239 contribution by Reichard *et al.* [17] in this issue) for thinking about the evolution of parental care. In
240 the final paper of this special issue, Cotter *et al.* [41] use the concept of host defences as a social good

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3 241 to ask whether viewing brood parasitism through the lens of social immunity can help to inform our
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5 242 understanding of social defences.

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9 244 **4. TINBERGEN'S CUCKOOS**

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12 246 Over 50 years ago, Niko Tinbergen published his landmark paper that provided a framework for
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14 247 integrative studies into behaviour [52]. Here he suggested that to fully comprehend how and why a
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16 248 trait evolves we must address 'Four questions' regarding: (i) the mechanisms that facilitate the trait,
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18 249 (ii) the developmental environment that alters expression of the trait, (iii) the fitness consequences of
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20 250 a trait, and (iv) the similarities and differences of the trait across a phylogeny. Arguably, research into
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22 251 brood parasite evolution has focused mostly on fitness consequences (that is, "Question Three"), a
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24 252 bias that is not unusual in the study of animal behaviour ([38,53]). This has led to great advances in
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26 253 our understanding of the requisite adaptations of parasites and counter-adaptations for host defences
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28 254 (e.g. birds [8], ants [54], bees [55], wasps [56]). Comparatively less attention has been given to
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30 255 understanding these adaptations from a mechanistic viewpoint, the role of the developmental
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32 256 environment in shaping adaptations, or how they vary across species and time, although recent
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34 257 research trends suggest this is changing. These questions are becoming ever more timely, particularly
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36 258 in the context of our increasing appreciation for the role of phenotypic plasticity (such as learning and
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38 259 development) in the evolutionary process [57–59], and in the context of the pressing need to
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40 260 understand and foresee how populations will respond to rapid environmental change [60]. For brood
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42 261 parasitism research, therefore, the time seems ripe to revisit Tinbergen's proposed framework. The
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44 262 studies and reviews in this special issue all cover one or more of Tinbergen's Four Questions (Table 1);
45
46 263 for example, McClelland *et al.* [61] demonstrate how combining analyses of mechanisms across taxa
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48 264 sheds light on the traits that may make brood parasitic birds successful; Cohen *et al.* [18] examines
49
50 265 the ontogeny of brood parasitic catfish and non-parasitic congeners to show that advanced
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52 266 development in this system is not an adaptation for parasitism, as we might expect if we only
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54 267 compared it against its host; and Medina & Langmore [62] link field experiments with evolutionary
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56 268 comparative analyses across hosts of brood parasitic birds to test how population density influences
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58 269 fitness. We hope this encourages future research that integrates mechanism, development and
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60 270 phylogeny with the fitness consequences of traits to understand brood parasitism evolution.

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57 272 **5. CONCLUSION**

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3 274 For many of us, brood parasitism is the perfect marriage of natural history and evolutionary biology.
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5 275 Yet at present, it is possible that our knowledge of natural history is more limiting of our efforts to
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7 276 fully address evolutionary questions, than ideas or methods may be. It is striking that a recent
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9 277 explosion of studies on new study systems has given us new insights, both challenging long-standing
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11 278 ideas in some cases (for example, that chick rejection cannot evolve [63–65]), and providing support
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13 279 for long-standing hypotheses in others (for example, the role of maternal inheritance in the faithful
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15 280 transmission of parasitic specialisation [66–68]). In the avian brood parasites, increasing work on
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17 281 tropical and south-temperate species in Asia, Australasia, Africa and South America has been
18
19 282 enlightening, as selection pressures in these regions are often quite different to those of the classic
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21 283 systems of northern hemispheres, owing to long and relatively faithful reproductive lives which
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23 284 present more opportunities for learning in defence, and likely shift the costs and benefits of defensive
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25 285 decisions in any one breeding attempt. Outside of birds, insights into the diverse systems in social
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27 286 insects and other animals also rely on devoted researchers collecting valuable natural history data.
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29 287 For example, the past decade has seen the discovery of several new species of inquilines of attine
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31 288 fungus-growing ants [69,70], including one in the process of speciating from its host [71]. Looking
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33 289 ahead, we hope that adventurous biologists continue to uncover the natural history of the many brood
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35 290 parasites about which tantalisingly little remains known, and perhaps even discover brood parasitism
36
37 291 for the first time in new taxa.

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36 293 **Additional Information**

37 294

39 295 **Data accessibility**

40 296 Search results used for the bibliometric analysis are available in the supplementary material.

41 297

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54 304

56 305 **Authors' Contributions**

57 306 RT conceived and carried out the bibliometric analysis; all authors wrote the manuscript.

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4
5 309 'We have no competing interests.'

6 310

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475 Table & Figure Legends

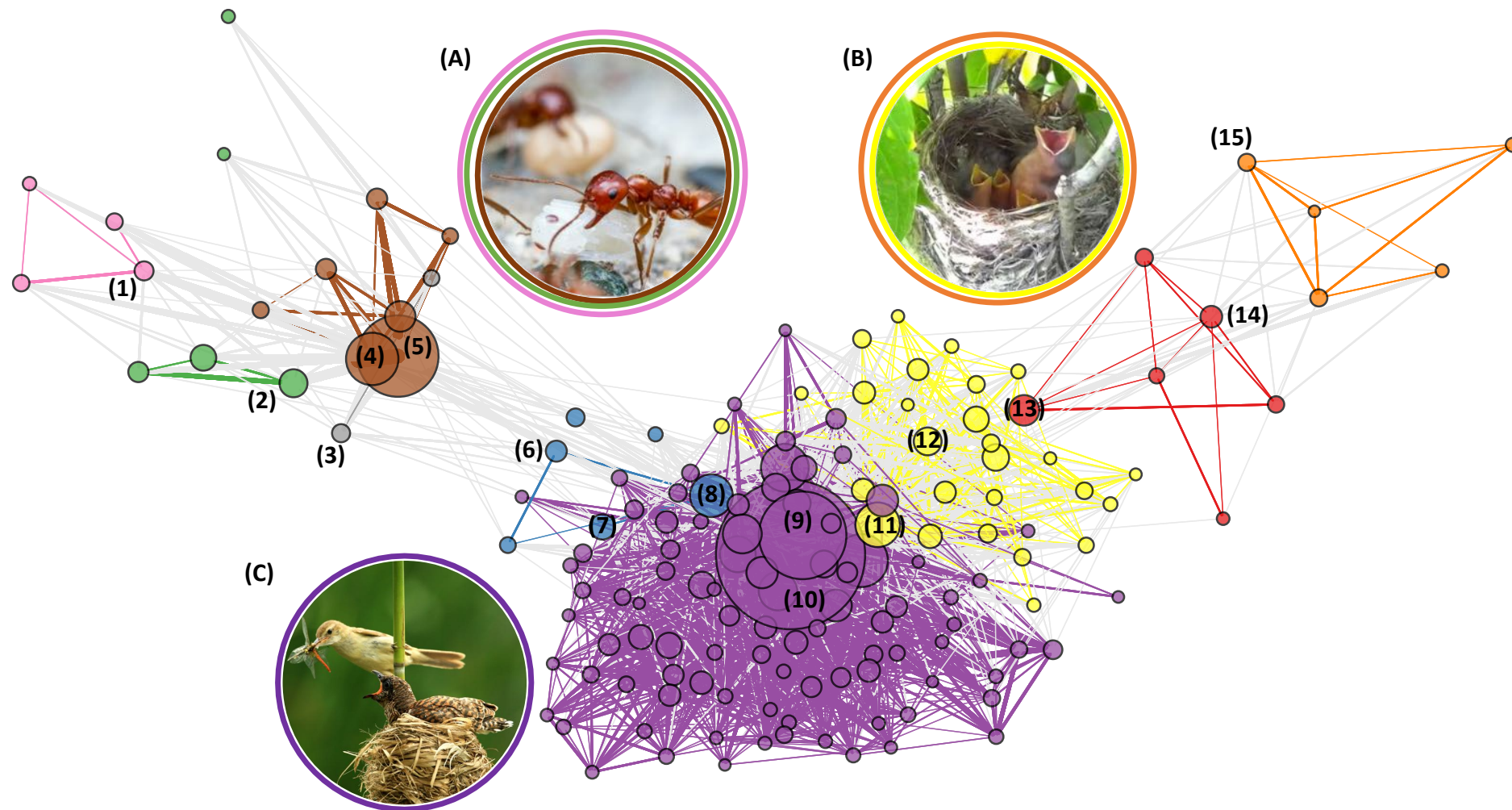
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477 Figure 1: Co-citation network of brood parasitism publications. The top 10% of co-cited documents
478 from a *Scopus* search are plotted using a Fruchterman layout; nodes represent co-cited
479 documents with key publications labelled (first author and year published given at bottom),
480 and edges represent co-citations (thickness indicates frequency). Node and edge colour
481 represent communities assigned by a walktrap clustering algorithm, and pale grey edges
482 represent links among these communities. inset photos show the main taxa associated with
483 the coloured co-citation communities: A. slave-makers *Polyergus mexicanus* with captured
484 pupae of host, *Formica subsericea* (Alex Wild Photography); B. Shiny cowbird *Molothrus*
485 *bonariensis* begs in the nest with chalk-browed mockingbird *Mimus saturninus* host nest-
486 mates (R. Gloag); C. Eurasian reed warbler, *Acrocephalus scirpaceus*, feeds common cuckoo
487 *Cuculus canorus* chick (Shutterstock). The grey community to the left represents
488 coevolutionary theory and integrative review papers, while the red co-citation community
489 represents statistical and modelling methods.

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491 Table 1. Contributions to this special issue according to Tinbergen's Four Questions framework [52]
492 for integrative studies (summaries of each question from [72]) and examples of broad
493 questions in each category that inform our understanding of the coevolutionary biology of
494 brood parasitism. Note that some contributions address more than one question.

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(1) Bourke 1991, (2) Buschinger 1986, (3) Nash 2008, (4) Wilson 1971, (5) Hölldobler 1990, (6) Thompson 1994, (7) Kilner 2011, (8) Dawkins 1979, (9) Rothstein 1990, (10) Davies 2000, (11) Rothstein 1975, (12) Friedmann 1929, (13) Burnham 2002, (14) Ricklefs 1969, (15) Robinson 1995

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1 Table 1. Contributions to this special issue according to Tinbergen's Four Questions framework [52]
2 for integrative studies (summaries of each question from [72]) and examples of broad questions in
3 each category that inform our understanding of the coevolutionary biology of brood parasitism.
4 Note that some contributions address more than one question.

'4 Questions'	Special issue contributions	Example research questions:
(i) Mechanism "How does it work?"	Stoddard <i>et al.</i> [42]	<i>What cognitive rules do hosts use to distinguish</i>
	Liang <i>et al.</i> [43]	<i>kin from non-kin?</i>
	Foitzik <i>et al.</i> [45]	<i>What molecular mechanisms underpin</i>
	Hanley <i>et al.</i> [46]	<i>parasite adaptations?</i>
	McClelland <i>et al.</i> [61]	<i>How are host defences constrained by sensory mechanisms?</i>
(ii) Development "How does it develop?"	Cohen <i>et al.</i> [18]	<i>Does rearing environment influence plasticity of</i>
	Foitzik <i>et al.</i> [45]	<i>defences?</i>
	McClelland <i>et al.</i> [61]	<i>Do parasites learn to recognise suitable hosts</i> <i>during development via imprinting?</i> <i>How do brood parasites overcome</i> <i>developmental constraints?</i>
(iii) Function "What is it for?"	Reichard <i>et al.</i> [17]	<i>What adaptations are necessary for parasites</i>
	Litman [23]	<i>to succeed?</i>
	Liang <i>et al.</i> [43]	<i>How do parasites differ in morphology,</i>
	Spottiswoode & Busch [44]	<i>behaviour and physiology to non-parasites?</i>
	Nash <i>et al.</i> [51]	<i>Why do counter-adaptations used by hosts to</i>
	Medina & Langmore [62]	<i>defend against parasites vary?</i>
(iv) Evolution "How did it evolve?"	Riehl & Feeney [14]	<i>How readily can parasites switch hosts?</i>
	Cohen <i>et al.</i> [18]	<i>Are the outcomes of coevolutionary arms'</i>
	Cini <i>et al.</i> [22]	<i>races predictable?</i>
	Gloag & Beekman [30]	<i>When does inclusive fitness theory predict the</i>
	Cotter <i>et al.</i> [41]	<i>evolution of parasitism in social groups?</i>
	Suhonen <i>et al.</i> [50]	
	McClelland <i>et al.</i> [61]	
	Medina & Langmore [62]	