

Review



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Monogamy without parental care? Social and genetic mating systems of avian brood parasites

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Classic evolutionary theory predicts that monogamy should be intimately linked with parental care. It has long been assumed, therefore, that avian brood parasites—which lay their eggs in the nests of ‘host’ species and provide little, if any, parental care—should be overwhelmingly promiscuous. However, recent studies have revealed that the social mating systems of brood parasites are surprisingly diverse, encompassing lek polygyny, monogamy, polygamy and promiscuity. What ecological or phylogenetic factors explain this variation, and why are some brood parasites apparently monogamous? Here we review the social and genetic mating systems of all 75 brood parasitic species for which data are available and evaluate several hypotheses that may help explain these patterns. We find that social monogamy is widespread, often co-occurring with territoriality and cooperative behaviour by the mated pair. Comparative studies, though preliminary, suggest that in some species, monogamy is associated with low host density and polygamy with higher host density. Interestingly, molecular data show that genetic and social mating systems can be entirely decoupled: genetic monogamy can occur in parasitic species that lack behavioural pair-bonds, possibly as a by-product of territoriality; conversely, social monogamy has been reported in parasites that are genetically polygamous. This synthesis suggests that social and genetic monogamy may result from very different selective pressures, and that male–female cooperative behaviours, population density and territoriality may all interact to favour the evolution of monogamous mating in brood parasites. Given that detailed descriptive data of social, and especially genetic, mating systems are still lacking for the majority of brood parasitic species, definitive tests of these hypotheses await future work.

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

1. Introduction

Classic theory predicts an association between mating system and parental care, with investment in dependent offspring expected to favour monogamy over promiscuity [1,2]. This hypothesis has received broad support across diverse taxa, especially with regards to social monogamy [3–5]; however, it is becoming clear that this association is more complex than initially supposed and major questions remain [4,6,7]. In addition to being associated with pair-bonding, the costs of tending offspring can also favour the establishment of family groups or other more complex social arrangements that support multiple individuals jointly contributing to the raising of offspring [8,9]. Increased sociality can consequently affect the intensity of sexual selection within a population [10–12] and shape the evolution of traits [13,14] and species [15,16] alike. It is perhaps unsurprising, therefore, that the study of mating system evolution

is an active and dynamic field of research within behavioural and evolutionary ecology [17,18].

Early behavioural estimates supported the hypothesis that parental behaviours and mating systems are linked in birds: Lack [2] estimated that over 90% of bird species form pair-bonds and suggested that polygamous or promiscuous mating systems should evolve only in species with precocial offspring that require little or no parental care. Since then, however, the development of genetic parentage techniques has revolutionized our understanding of avian mating systems and challenged this hypothesis [6]. Where genetic and social monogamy are tightly linked in some taxa, such as mammals [7], molecular techniques have revealed that the majority of socially monogamous birds are not genetically monogamous (more than 75% [6]). Therefore, while estimates of the prevalence of social monogamy across avian lineages have not dramatically changed since Lack's early work (approx. 80% of bird species are now thought to be socially monogamous [19]), the absence of a link between social and genetic mating systems in birds raises questions about the nature and causality of the observed relationship between parental care and mating system evolution.

Obligate brood parasites, which lay their eggs into the nests of other birds and foist the cost of parental care onto the 'host', may provide unique insights into the selective pressures shaping mating systems. Studies of these systems have largely focused on the coevolutionary interactions between brood parasites and their hosts [20–22]; however, although brood parasitism is a relatively widespread reproductive mode, occurring in approximately 100 bird species in seven lineages across the avian phylogeny [23], researchers have tended to neglect enquiry into other aspects of their life-histories. For example, contrary to theoretical predictions that brood parasitic birds should be universally promiscuous because they are freed from the constraints of parental care, both behavioural and genetic evidence shows that brood parasitic birds exhibit a bewildering diversity of reproductive strategies. This variability was highlighted in an early review by Barnard [24], who concluded that the range of mating patterns observed in brood parasitic birds, particularly the prevalence of pair-bonding behaviours, simply could not be reconciled with existing paradigms. Along the same lines, Hauber & Dearborn [25] found that the three brood parasitic species for which molecular data were then available (brown-headed cowbirds (*Molothrus ater*), common cuckoos (*Cuculus canorus*) and great spotted cuckoos (*Clamator glandarius*)) were all primarily territorial and exhibited both social and genetic monogamy [26–32]. Hauber & Dearborn's [25] review also found that all three species exhibited plasticity in their mating systems across the population (ranging from territorial and monogamous to non-territorial and polygamous), suggesting adaptive flexibility in response to local ecological conditions.

Since the early reviews of Barnard [24] and Hauber & Dearborn [25], our knowledge of brood parasite social and genetic mating systems has increased steadily. Field-based research is unveiling the behaviour and ecology of a greater diversity of parasites throughout the Afrotropics, Australasia and the Neotropics, and in some cases is using genetic tools to investigate sibship cohorts and reconstruct mating patterns (e.g. [33]). In this review, we aim to bring together all available behavioural and genetic evidence on brood parasite mating systems and integrate it into theory on the evolution

of mating systems and parental care (electronic supplementary material, table S1). We then discuss patterns that emerge from these data in the context of several non-mutually exclusive hypotheses to explore why various mating systems may evolve in brood parasites, and evaluate the evidence for these hypotheses in the seven avian lineages that have independently evolved obligate parasitism.

2. Literature review

For the 101 species currently recognized as obligate brood parasites, we searched the primary and secondary literature for information on social mating system, territorial behaviours, number of host species, and genetic data on parentage and mating patterns. When available, we noted reports of behaviours that might be relevant to pair-bonding or territoriality, such as courtship displays, feeding of conspecific fledglings by parasitic adults and male–female cooperation in searching for host nests or distracting hosts during laying. Of these 101 species, we found data on 75, including: descriptions of territorial behaviour (71 spp.), social mating system (56 spp.) and genetic mating system (5 spp.). Species from all seven lineages of avian brood parasites are represented in this dataset (electronic supplementary material, table S1).

3. General patterns

Several important patterns emerge from this review (electronic supplementary material, table S1). First, many brood parasites exhibit some degree of pair-bonding—at least 34 of 75 species (45%), although this estimate may be highly skewed by the amount of missing data. Cooperative behaviours by male–female pairs are surprisingly widespread, having been recorded in five of seven parasite lineages (the exceptions being the Neomorphine cuckoos (*Tapera*, *Dromococcyx*) and the indigobirds (*Viduidae*)). These (apparently) short-term associations are most evident through cooperative nest searching or cooperative parasitism events. Longer-term pair-bonds, resembling social monogamy, have been described in six of seven parasitic lineages, including black-headed ducks (*Heteronetta atricapilla*), many cuckoo genera (*Clamator*, *Chrysococcyx*, *Chalcites*, *Tapera* and *Cuculus*), some honeyguides (*Protodiscus*, *Indicator*) and some cowbirds (*Molothrus*).

With the exception of the viduid finches, which are exclusively promiscuous, social mating systems are variable within clades, and, in many cases, across populations of the same species [31,34]. This general variability is consistent with ecological flexibility rather than phylogenetic conservatism. Under the broad umbrella of 'social monogamy', the strength and duration of behavioural pair-bonds also vary across species. For example, social monogamy is often inferred from the observation that brood parasites are usually observed in pairs during the breeding season (e.g. [35–37]) and exhibit behaviours such as duetting, courtship feeding and territory defence [38,39]. Such observations are typically conducted on unmarked individuals, making it difficult to ascertain whether pair-bonds span courtship, copulation and egg-laying (indicative of serial or sequential monogamy) or for the entire breeding season.

Perhaps the most striking pattern to emerge (electronic supplementary material, table S1) is that territoriality is clearly the rule in brood parasitic birds rather than the exception. In fact, the majority of species for which data are available exhibit some form of territorial defence. In the parasitic finches (*Anomalospiza* and *Vidua*), *Indicator* honeyguides, and many cuckoos (*Cacomantis*, *Chalcites*, *Chrysococcyx*, *Clamator*, *Cuculus*, *Heteroscenes* and *Tapera*), males call or sing from regular sites throughout the breeding season that are visited by females (electronic supplementary material, table S1). In shaft-tailed whydahs (*Vidua regia*) and yellow-rumped honeyguides (*Indicator xanthonotus*), territories are centred around discrete resource patches (water sources and bee hives, respectively [40,41]), whereas in many cuckoos males appear to defend exclusive 'laying territories' or home ranges in which the resource being defended is presumably access to host nests. The degree of social bonding between males and females varies widely across these territorial systems, ranging from the promiscuous associations of indigobirds (in which females visit several male song posts before mating) to the extended behavioural pair-bonds of some *Chrysococcyx* cuckoos [38].

4. Hypotheses and evidence

The patterns mentioned above are unquestionably preliminary, given that the natural history of most brood parasites is poorly described. Nevertheless, it is clear from the above summary that many species exhibit a suite of male–female social interactions that are inconsistent with promiscuity. This review suggests that both social and genetic monogamy are surprisingly common in brood parasites, and that pair-bonding often co-occurs with territoriality and cooperative behaviours by males and females. In the following section, we interpret these patterns in the context of non-mutually exclusive hypotheses regarding the evolution of avian mating systems. Given that both brood parasitism and monogamy have several independent origins, different selective pressures have likely shaped the evolution of mating behaviours across lineages. Therefore, our discussion of each hypothesis focuses on the species for which relevant data are available, and is intended to stimulate future research rather than provide definitive evaluations.

(a) Phylogenetic history

Variation in avian social behaviours, including social mating system and extra-pair paternity, is known to have a strong phylogenetic component [6,42]. Given that reproductive behaviours are not solely determined by adaptive plasticity, the view that the mating systems of brood parasites reflect phylogenetic history is a valid null hypothesis to adaptive alternatives. The influence of phylogeny on behaviour is obvious in some clades of brood parasites. Viduid finches (*Vidua* and *Anomalospiza*), for example, represent a relatively recent radiation of 20 species (less than 5 Ma) that share a promiscuous mating system in which males attract females by singing from conspicuous perches, in addition to many exhibiting morphological and plumage similarities [43]. On the other hand, closely related species in other clades vary markedly in their breeding systems, suggesting that mating systems are not always constrained by recent evolutionary history. The six *Molothrus* cowbirds, which also diverged

recently (less than 3–5 Ma), vary widely in social and genetic mating system (electronic supplementary material, table S1, [44]); and well-documented variation among and within populations of the brown-headed cowbird suggest adaptive plasticity rather than phylogenetic inertia [31,45]. Mating systems in the most species-rich parasitic lineage, the cuculine cuckoos, appear similarly variable (electronic supplementary material, table S1). Furthermore, no clear patterns emerge as to the ancestral mating systems of parasitic lineages (electronic supplementary material, table 2). Although some brood parasitic lineages are embedded within larger clades in which social monogamy is the rule (including viduid finches and New World cuckoos), in other clades the mating systems of sister lineages vary from monogamous to polygynous to promiscuous (electronic supplementary material, table S2). Rigorous assessment of the role of phylogeny in parasite mating systems must remain a challenge for the future, because such an analysis would require substantially more information about ecology and life history of a species-rich parasitic clade than is currently available. Nevertheless, evidence in support of any of the adaptive hypotheses presented below should be interpreted in the context of the evolutionary history of the taxon in question, and evaluated against the null hypothesis that variation in mating system may simply have little effect on individual fitness.

(b) Population density

Theory predicts that monogamy can evolve only when the benefits of guarding a mate outweigh the costs, leading to the prediction that monogamy should be more prevalent when mates are widely dispersed or difficult to find (either because the overall population density is low or because the operational sex ratio is highly biased [11,46]). Although no studies have yet attempted to quantify population density across species of brood parasites, intraspecific comparisons offer limited support for this hypothesis. In all three species for which comparative data are available—pin-tailed whydahs (*Vidua macroura*), brown-headed cowbirds and great spotted cuckoos—increases in population density were associated with increased levels of polygamous mating [30,32,34,47]. Interpreting these patterns in light of the mate-guarding hypothesis is less straightforward than it might seem, however, because this correlation might be confounded by host population density in unpredictable ways. Spatial clustering of hosts might favour a polygamous system in which males defend resources rather than mates (as in the colonially nesting hosts of giant cowbirds, *Molothrus oryzivorus* [48]); whereas rare, widely dispersed hosts might favour large female home ranges that make it harder for males to defend them [40]. Given that host and parasite densities are not necessarily independent, correlational studies alone are insufficient to disentangle these effects.

The lack of concordance between genetic and social mating patterns poses an even greater challenge to the notion that social monogamy might represent a flexible adjustment to low population densities. Bolopo *et al.* [34] noted that behavioural pair-bonds persisted throughout the breeding season in a high-density population of great spotted cuckoos, although parentage analyses revealed a high rate of polygamous mating (greater than 75%). Conversely, normally promiscuous pin-tailed whydahs copulated with fewer partners at low population densities, but they failed

to form behavioural pair-bonds even when the number of available mates was severely limited [40]. Brown-headed cowbirds routinely form monogamous consortships in captive aviaries and mate exclusively within the consortship, even when population densities within the aviaries are high enough that promiscuous mating is possible ([49], D. White 2018, personal communications). These studies suggest that genetic mating patterns of brood parasites are more sensitive to proximate changes in mate availability than social mating patterns. If so, this would be consistent with within-species comparisons of socially monogamous, non-parasitic birds, in which rates of extra-pair copulations often increase with population density [50], but they do not resolve the larger question of why social pair-bonds occur in brood parasites in the first place.

(c) Territoriality

Like population density and sex ratio, territorial behaviour by members of either sex is predicted to influence their spatial distribution, and hence the potential for economic mate monopolization [11]. Although territorial behaviour of some form is widespread in brood parasitic birds, the degree of social bonding between males and females varies widely across systems (electronic supplementary material, table S1). From the perspective of mating system evolution, the crucial difference lies in whether territoriality results in spatial clustering or dispersion of mates: male display sites may be spatially clustered, leading to an 'exploded' or dispersed lek-like mating system; whereas territories that encompass several host nests are typically large, leading to spatial dispersion. Defence of exclusive home ranges by female parasites, for example, might favour monogamous mating by males if the costs of travelling across territories and searching for additional mates are sufficiently high. Genetic and radio-tracking studies support this prediction in Horsfield's bronze-cuckoos (*Chalcites basalis* [33]) and striped cuckoos (*Tapera naevia*, M. Mark unpublished data in [51]), in which females defend exclusive breeding territories and mate monogamously. Males in these species may be monogamous or sequentially monogamous, staying with a female for the duration of her reproductive bout. Behavioural observations suggest a similar pattern in several other cuckoo genera, including *Cacomantis*, *Heteroscenes* and *Chrysococcyx* (electronic supplementary material, table S1). However, radio-tracking data are available for relatively few brood parasites, and in most species females appear to overlap in their host use rather than defend exclusive territories (including screaming and shiny cowbirds (*Molothrus rufoaxillaris* and *M. bonariensis*) [52] and common cuckoo [53]).

Even in the absence of behavioural pair-bonds, territorial behaviours by either sex could alter genetic mating patterns by constraining the number of mates available to a parasite exploiting host nests in a given area. This may explain the apparently puzzling pattern of genetic monogamy by females in some species that lack behavioural pair-bonds [33]. Territoriality also increases the probability that adults will be genetically related to parasitic offspring fledged from host nests within their territories, potentially explaining the surprisingly common observations of provisioning and prolonged social associations between parasitic adults and offspring after fledging ([54,55]; see below).

(d) Parental care/assistance

While it is widely acknowledged that brood parasites provide little or no parental care following deposition of their egg in the host nest, evidence for (or suspicion of) limited parental care does exist in several brood parasite lineages, such as cuckoos, cowbirds and honeyguides. Notably, brown-headed cowbirds and great spotted cuckoos have been recorded to exhibit 'mafia' behaviours, in which the parent brood parasite monitors its egg in the host nest and punishes egg rejection behaviours by the host repeatedly until the egg is accepted [55,56]. These behaviours should only exist in systems where the nestling parasite requires parental care, and it does not entirely destroy the host's reproductive output following hatching [57], suggesting that this behaviour could also exist in other brood parasite lineages, such as other *Clamator*, *Eudynamis* and *Scythrops* cuckoos, *Molothrus* cowbirds and the parasitic finches. However, only female great spotted cuckoos and brown-headed cowbirds have been reported to exhibit this behaviour. In both species, females also hold and defend territories (see references within [55,56]), but mating systems of both species range from social and genetic monogamy to polygamy (electronic supplementary material, table S1). Therefore, while some evidence of extended parental behaviour exists in these species, there is little evidence of male assistance, which may indicate little potential impact of this behaviour on mating system evolution.

Evidence of adult brood parasites feeding fledged juveniles is also surprisingly common, with records of this behaviour in over 10% of brood parasite species (at least 13 species in total [37,38]), spanning all three cuckoo lineages (*Cacomantis*, *Chrysococcyx*, *Clamator*, *Cuculus*, *Eudynamis*, *Heteroscenes*, *Tapera*) as well as cowbirds (*Molothrus*) and one possible record in an *Indicator* honeyguide. Interestingly, this behaviour has been observed in both male and females alone or together and in some cases across multiple days [38]. Further, one study suggests that post-fledgling juvenile brown-headed cowbirds are significantly more likely to associate with their mothers than non-related females [58]. While the majority of species in which this behaviour has been recorded also exhibit social monogamy and courtship feeding, this is not universally the case [37]. The majority of these species also exhibit evidence of territoriality (electronic supplementary material, table S1 [38]). Taken together, this may suggest that extended biparental behaviours exist in some brood parasite species, possibly because territoriality restricts the opportunity for polygamy. Considering the general lack of natural history data on the majority of brood parasites, this unintuitive constraint on parasitic mating systems may be more widespread than currently appreciated.

(e) Coordination/cooperation between male and female in reproductive behaviours

Successful parasitism requires a brood parasite to both accurately locate a host's nest and successfully deposit an egg in it at an appropriate time. Hosts can minimize the likelihood of their nest being discovered by building nests that are difficult to locate [59] or deceptive [60,61], and can defend access to a nest through behaviours such as vigorous mobbing [62,63] or blocking access ([64,65]; for a more detailed discussion of interactions at this stage of the nesting cycle, see [66,67]). Considering the key importance of nest location and egg

deposition for brood parasite reproductive success [66], selection may favour male–female cooperative behaviours, which may either be a result of, or consequently influence the parasite’s social and genetic mating system and constrain polygamous behaviours.

Cooperative nest searching behaviours have been reported in several brood parasite lineages, but are especially evident in the cowbirds, which are more abundant and more conspicuous around host nests compared to other brood parasite lineages. Cooperative nest searching may result from several different behavioural processes, each of which might have repercussions for social and genetic mating patterns. For example, in species where males hold territories and monitor host nests within their territories, one or multiple females might mate with males in exchange for access to nests (as suspected in brown-headed cowbirds [30]). Monopolization of host nests within a male’s territory should interact with the density of both parasite and host populations, potentially resulting in social and genetic mating patterns that span monogamy to polygamy. Alternatively, in screaming cowbirds and black-headed ducks (*Heteronetta atricapilla*), the two species for which long-lasting pair-bonds have been documented, male–female pairs routinely search for host nests together: male screaming cowbirds typically accompany females when visiting host nests [52], and male black-headed ducks may even take the lead in locating host nests [68]. In these instances, cooperation may be a consequence of pre-existing male–female pair-bonding behaviours, rather than a driver. Regardless of the direction of this relationship, such behaviours should decrease the female’s opportunity for extra-pair mating, thus promoting social and genetic monogamy [50]. While the overall sparsity of these kinds of baseline natural history data makes it difficult to generalize, these examples suggest that cooperative nest searching behaviours might interact with parasite and host density, and influence patterns of social and genetic mating systems in brood parasites.

Cooperation during egg-laying, when the male apparently assists the female in gaining access to a host nest by drawing the attention of the hosts away from the female, has been reported in many cuckoo genera (*Clamator*, *Chrysococcyx*, *Cuculus*, *Eudynamys*, *Scythrops*, *Pachycoccyx* and *Cacomantis*), as well as in cuckoo-finches (*Anomalospiza imberbis*), lesser honeyguides (*Indicator minor*) and giant cowbirds (electronic supplementary material, table S1). Similar to cooperative nest searching, these behaviours may be a product of, or promote, short- or long-term monogamy in cooperating pairs. However, while these kinds of behaviours have long been noted in natural history observations on unmarked individuals (such as when, in 1910, Frank Finn noted that ‘Mrs Fraser saw the male [common] cuckoo decoy away the angry small birds while his mate deposited the egg’ [69]), recent video-based studies place the general reliability of these observations in question, especially in monomorphic brood parasite species. In two video-based studies, which investigated laying behaviours of shiny cowbirds [70] and great spotted cuckoos [71], females were regularly recorded to ‘shadow’ other laying females who drew the host’s aggression, which might closely resemble a male-instigated ‘distraction’ display. Therefore, while distraction displays appear to have been reliably documented in some species, such as great spotted cuckoos [71,72], the potential unreliability of these data make it difficult to

contemplate whether this behaviour is common enough to influence social and genetic mating patterns.

(f) Mate choice

Although studies of mating system evolution have traditionally framed adaptive hypotheses from the perspective of male fitness, recent work has demonstrated that female behaviours—including female song, territoriality and mate choice—can play an equally important role [50,73]. For example, radio-tracking and genetic studies of species with biparental care have found that pair-bonded females may actively seek copulations with extra-pair males, potentially choosing extra-pair mates that are genetically superior to their social mates [74], or genetically more or less similar to themselves [75]. Although female fitness interests may align with those of males in some systems, in others it is possible that sexual conflict might lead to mating patterns that are not necessarily advantageous to both sexes.

In brown-headed cowbirds, the only brood parasite for which data on mate choice are available, playback experiments have demonstrated that captive females are remarkably consistent in their preferences for courtship songs by different males [76]. The strength of this preference is correlated with independent measures of male social dominance, suggesting that females are able to use male song to infer some aspect of male quality [77,78]. However, although most females apparently prefer to mate with a minority of males, pairs typically form monogamous consortships in captivity—potentially reflecting mate-guarding or mate competition by females as well as choice by males [79,80]. Recent experimental work has emphasized the importance of female choice in maintaining these bonds: female cowbirds who received lesioning of the HVC nucleus of the brain (an area associated with song learning and production) no longer discriminated between the songs of male cowbirds, and no longer participated in monogamous consortships [81]. White *et al.* [80] found that experimental removal of adult males from captive flocks resulted in a similar breakdown of consortships and promiscuous mating by juvenile males. Taken together, these captive studies suggest that social demographics, including movement patterns, sex ratios and age composition within communities of available mates, play an important role in mating patterns in brown-headed cowbirds; and that these patterns are mediated through proximate mechanisms involving both male and female choice and competition for mates. Whether the same patterns hold true in wild populations or in other species of brood parasites is not known, but they provide tantalizing avenues for future research.

5. Future directions

In this review, we have argued that brood parasitic birds provide unique models for investigating the selective pressures shaping social and genetic mating systems. While the diversity and drivers of brood parasite mating systems have been discussed previously [24,25], our synthesis suggests that several selective pressures aside from parental care, including territoriality, population density, mate choice and cooperative behaviours by mated pairs, can favour monogamous mating and/or behavioural pair-bonding. These findings have broad implications for mating system evolution

in other egg-laying taxa that lack parental care, including insects, fish, and reptiles and amphibians. Brood parasites across taxa face similar challenges—such as the need to locate and monitor host nests and defend them against other parasites—which may shape mating patterns in similar ways. More information is needed on the population densities, demography, territorial behaviours and mating patterns of other reproductive parasites to understand whether the correlations highlighted here can yield insights in other taxa. Our review also emphasizes that, even within birds, no single explanation is sufficient to explain mating patterns across brood parasitic lineages. Definitive hypothesis tests are clearly lacking for the hypotheses presented here, and in most cases basic descriptive data are not yet available. Here, we suggest several fruitful avenues for future research with regards to the ecology and evolution of brood parasite mating systems.

Perhaps most notably, the results of this review highlight the potential for researchers studying host species to opportunistically collect genetic data on brood parasitic offspring. These data would take relatively little effort and minimal additional cost at the time in the context of ongoing research into host species, but would be difficult to justify as a primary study objective. Given that studies have successfully gained insights into the social and genetic mating patterns of brood parasites solely using blood samples obtained from brood parasite chicks from within host nests (e.g. [33]), and that genetic mating patterns can vary within species [27,34], we implore researchers to collect genetic samples from juvenile cuckoos (as well as maternal DNA samples from discarded eggs, if possible) to facilitate similar studies on a more geographically and phylogenetically diverse spread of brood parasite species. Thanks to the recent development of rapid, low-cost methods of identifying single-nucleotide polymorphisms as neutral genetic markers [82,83], genetic assignment of egg maternity and sibling relationships no longer requires the laborious development of species-specific microsatellites. Collection of genetic samples, rather than their analysis, should now be viewed as the limiting factor in molecular studies of brood parasite mating systems. Combining these new sequencing approaches with older methods of assigning egg maternity (such as individually recognizable shell patterns or maternally inherited mitochondrial markers) could enable molecular determination of extra-pair parentage even when it is not feasible to capture adult parasites.

The incorporation of new technologies might also enable novel insights into brood parasite natural history and reproductive ecology. For example, while important insights have been gained through radio-telemetry (e.g. [52,53,84]) the technological advances, miniaturization and continually decreasing price of satellite-tracking units are opening the possibility of using these technologies to track the movements of individual brood parasites both inside and outside of their breeding seasons (e.g. [85]). The use of this technology could vastly improve our understanding of brood parasite movement behaviours, which could better inform our knowledge of their nest searching strategies, home range sizes, territoriality, social behaviours and site fidelity. A major advantage of this technology over other tracking methods is that data can be obtained remotely, without the need to recapture the target individual. Further, while perhaps logistically difficult, the use of continuous-recording units that can be attached to individual birds [86] might also provide new insights into brood parasite social behaviours. This technology has not previously been used and could prove particularly informative for species in which lekking behaviours are suspected (electronic supplementary material, table S1); however, a major drawback is that the bird needs to be recaptured in order to download the data, perhaps making this a little far out of reach for the time being.

Finally, by compiling behavioural and genetic evidence, this review also highlights the stark lack of available information on the natural history of many brood parasite species (electronic supplementary material, table S1). Of the world's 101 brood parasite species, we found no information for 26 species, behavioural information on 75 species (many of these data comprise opportunistic observations on a limited number of individuals) and information on genetic mating systems for five species. We hope that this will help researchers identify what is and (more importantly) what is not known and enable both the opportunistic recording of ecologically interesting behaviours (including evidence of behavioural pair-bonding, measures of population density and territoriality) on species for which these data do not currently exist, and more detailed investigations of brood parasite species that are better studied.

Data accessibility. This article has no additional data.

Competing interests. We declare we have no competing interests.

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