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Article

From micro- to macroevolution: brood parasitism as a driver of phenotypic diversity in birds

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Abstract

A fundamental question in biology is how diversity evolves and why some clades are more diverse than others. Phenotypic diversity has often been shown to result from morphological adaptation to different habitats. The role of behavioral interactions as a driver of broadscale phenotypic diversity has received comparatively less attention. Behavioral interactions, however, are a key agent of natural selection. Antagonistic behavioral interactions with predators or with parasites can have significant fitness consequences, and hence act as strong evolutionary forces on the phenotype of species, ultimately generating diversity between species of both victims and exploiters. Avian obligate brood parasites lay their eggs in the nests of other species, their hosts, and this behavioral interaction between hosts and parasites is often considered one of the best examples of coevolution in the natural world. In this review, we use the coevolution between brood parasites and their hosts to illustrate the potential of behavioral interactions to drive evolution of phenotypic diversity at different taxonomic scales. We provide a bridge between behavioral ecology and macroevolution by describing how this interaction has increased avian phenotypic diversity not only in the brood parasitic clades but also in their hosts.

Key words: brood parasitism, coevolution, diversity, phenotypic variation, macroevolution

What drives the diversity of colors, shapes, and sizes that we see in the animal world? Environmental variables are known to play a fundamental role in the generation of phenotypic diversity. Adaptations to different habitats (benthic/limnetic, tree crown/ground) have led to the incredible morphological diversity of *Anolis* lizards, sticklebacks, and rockfish (Schluter 2000; Gillespie 2004; Losos and Ricklefs 2009; Ingram 2010). These clades have radiated into different regions of morphological space, evolving collections of traits that suit their particular habitat. We have known for years, however, that divergent selection on phenotypes is not only a function of the habitat of a species (Plotkin 1988; Lapiedra et al. 2013; Piaget 2013). Behavioral interactions can also be important drivers of

phenotypic diversity. The impact of behavioral interactions on evolution is expected because such interactions are ubiquitous, especially in animals, and they have major fitness consequences (Plotkin 1988; Piaget 2013). Behavioral interactions comprise how animals choose mates, compete for resources, defend themselves against predators and parasites, interact with their parents or offspring and more (Duckworth 2009).

There is evidence of how behavioral interactions have led to increased phenotypic diversity at different evolutionary scales (within species, between species). For instance, in guppies, sexual selection and differences in mating tactics between populations (e.g., polyandry vs. monogamy) can predict the amount of variation in

phenotypic traits (Barbosa et al. 2010). Males from polyandrous populations are significantly more variable than males from monogamous mating treatments, suggesting that sexual selection can drive the diversification of bright coloration patterns in male guppies (Barbosa et al. 2010). Similarly, selection imposed by predators is also suggested to have driven the evolution of color polymorphism in frogs and butterflies (Stimson and Berman 1990; Karpestam et al. 2016; Holmes et al. 2017). Differences in predator size and home ranges, at regional scales, can lead to phenotypic mosaics within prey species (Holmes et al. 2017). At a broader scale, variation in the strength of sexual selection in different species of toucans is correlated with differences in signal complexity and high phenotypic diversity within the clade (Miles and Fuxjager 2019).

Not all behavioral interactions are expected to lead to phenotypic diversification. Behavioral plasticity can shield traits from the effects of natural selection, relaxing selection for phenotypic change, and hence diversification (Duckworth 2009). For example, in the presence of predators, Caribbean lizards switched their habitat from ground to canopy to avoid predation (Losos et al. 2006). This relaxes selection for morphological traits that might otherwise evolve in response to predation, such as longer legs or faster phenotypes. Similarly, behavioral interactions can also favor convergent phenotypes, decreasing overall diversity. Predator selection for cryptic colorations has led to uniformity in color patterns in adult shore crabs and caterpillars, which present reduced diversity compared with other ontogenetic stages (Nokelainen et al. 2019; Medina et al. 2020). In general, however, it is thought that interactions with enemies (predators, parasites, competitors, dangerous prey) are more important evolutionary agents of selection than other types of interactions (Vermeij 1994; Vamosi 2005). These antagonistic behavioral interactions can lead not only to independent evolutionary responses in the organisms involved, but also to coevolution between the interacting parties (Yoder and Nuismer 2010; Hembry et al. 2014).

Coevolutionary interactions are defined as interactions that lead to reciprocal adaptations in the interacting parties, and some behavioral interactions are also examples of coevolution. Not all behavioral interactions, however, lead to coevolution, and not all coevolutionary interactions involve behavioral interactions. Some pollinator–plant interactions or endoparasite–host interactions are examples of coevolution, but they do not necessarily involve a behavioral interaction from both parties. Coevolutionary interactions have been suggested to have macroevolutionary effects and lead to species and phenotypic diversification over time (Yoder and Nuismer 2010; Hembry et al. 2014). Macroevolutionary processes are defined as long timescale phenomena that occur at or above the level of species, in contrast to microevolutionary processes, which occur within species or populations and over a short timescale (Brooks 1988). Despite the long-standing prediction that coevolution should lead to macroevolutionary effects (Darwin 1859; Klassen 1992), rigorous exploration of this path has only been possible in recent years, with the development of robust phylogenies and novel phylogenetic methods. Interestingly, there is still limited evidence supporting the role of coevolution in the generation of diversity at broad evolutionary scales (i.e., above the species level; Harmon et al. 2019; Week and Nuismer 2019). For instance, recent evidence of the importance of coevolution in diversity comes from studies done within species (Betts et al. 2018; Nair et al. 2019) and examples at broader scales are rare (Nunn et al. 2004; Weber and Agrawal 2014; Arbuckle and Speed 2015).

Theoretical work has given insights on how behavior could provide a key link between coevolution and evolutionary diversity.

Yoder and Nuismer (2010) analyzed simulations of coevolutionary antagonistic interactions that involve costly phenotype matching—where the exploiting species maximizes its fitness by matching the phenotype of its victim and this imposes a cost on the victim. They found that costly phenotype matching was more likely to lead to increased phenotypic diversity. Phenotype matching causes divergence between species of victims as selection favours morphs that are not matched by the exploiters and this in turn diversifies the exploiters, as they chase their victims through phenotypic space, over evolutionary time.

The results of Yoder and Nuismer's (2010) theoretical simulations match the coevolution of the obligate avian brood parasites and their hosts (Øien et al. 1995; Soler and Møller 1995). In this strongly antagonistic behavioral interaction, parasitic species lay their eggs in the nests of hosts and this has resulted in phenotype matching. Many species of hosts reject brood parasitic eggs based on their appearance, which has selected for parasitic eggs that mimic the eggs of their hosts and host eggs that evade such mimicry (Brooke and Davies 1988; Davies 2000; Krüger and Davies 2002; Stoddard and Stevens 2010). Changes in the extent of egg mimicry can occur in as little as 40 years (Spottiswoode and Stevens 2012). The reciprocal and fast-evolving phenotypic changes in hosts and parasites make avian brood parasitism an ideal system to assess the role of behavioral interactions in the diversification of both hosts and parasites.

In this review, we consider how brood parasitism can increase avian phenotypic diversity at three different levels (Figure 1): within species, among species, and between clades of species. Our aim is to 1) to collate information to gain greater insights into the role of brood parasitism in the generation of avian phenotypic diversity and 2) to synthesize information from microevolutionary studies to generate predictions at a broader phylogenetic scale.

The Study System: Avian Brood Parasitism

Obligate avian brood parasites lay their eggs in the nests of other species, their hosts, which take care of the foreign chicks (Davies 2000). Brood parasitism is a widespread interaction; almost 100 bird species are obligate brood parasites, and >500 bird species are

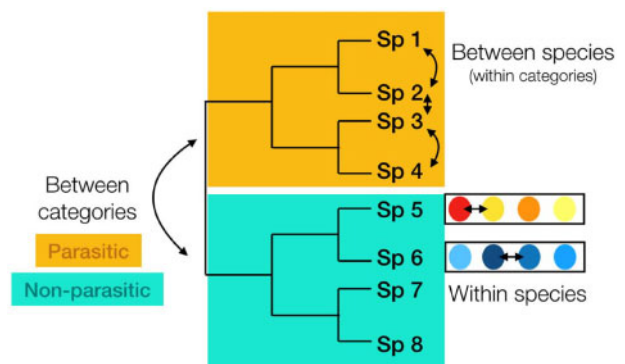


Figure 1. Examples of the 3 levels of variation explored in this review. We present examples of variation at the broadest evolutionary scale (between categories of host/nonhosts and parasites/nonparasites), intermediate evolutionary scales (*between species*), and at a microevolutionary scale (between populations or between individuals). Variation between categories (green vs. orange) does not need to involve comparisons between monophyletic groups, because, as discussed in the main text, host status is a trait that is scattered through the phylogeny.

considered as main hosts—with parasitism rates $>10\%$ (Friedmann 1955; Friedmann and Kiff 1985; Brooker and Brooker 1989b). Parasitism rates in some populations can reach 63% of hosts nests (Gloag et al. 2014) and even 91% (59/65 nests) in populations of the dickcissel *Spiza americana* (Hatch 1983). There is variation in the number of species exploited by different brood parasites. A recent study reported that while most old-world cuckoos species exploit fewer than 50 host species (belonging to <10 families), some species, such as the common cuckoo *Cuculus canorus*, exploit almost 200 species from >30 different families (Yang et al. 2020). Similarly, in the Americas, the screaming cowbird *Molothrus rufoaxillaris* uses a single host species, whereas the shiny cowbird *M. bonariensis* is known to use at least 176 species as hosts (Mason 1986). In Australia, species such as the shining bronze-cuckoo or the little bronze-cuckoo, *Chalcites lucidus* and *C. minutillus*, each specialize on one genus (and primarily exploit one species within that genus) (Brooker and Brooker 1990). The degree of host specialization in brood parasites is generally related to their geographic range size and the body size of the parasite, with larger parasites being able to exploit a wider range of hosts with different body sizes (Medina and Langmore 2016b). In general, most brood parasitic interactions involve very few species (sometimes only 2), unlike many other host–parasite interactions that involve several species, which makes it easier to isolate the source of selection, identify patterns, and test predictions (Rothstein 1990).

Studies of avian brood parasitism have been heavily biased toward the microevolutionary aspects of the interaction. This has resulted in detailed studies in >100 species of hosts and a thorough understanding of the precise mechanisms through which defenses evolve (Soler 2014). The less explored macroevolutionary aspects of brood parasitism have only been studied in depth in the last 20 years (Krüger and Davies 2002; Rothstein et al. 2002; Sorenson and Payne 2002, 2005; Payne 2005a)—although see Brooks (1988) and Klassen (1992)—and much less intensively. This is probably due to the fact that testing macroevolutionary hypotheses requires reliable phylogenies and suitable comparative methods.

Who needs to run faster?

The outcomes of coevolution between two interacting species depend on the costs of the interaction (Yoder and Nuismer, 2010). Dawkins and Krebs (1979) illustrate this principle with a quote from Aesop: “The rabbit runs faster than the fox, because the rabbit is running for his life while the fox is only running for his dinner.” There are strong selective pressures on both hosts and brood parasites. If hosts do not defend themselves against brood parasites, they may lose their current brood and if parasites do not exploit their hosts effectively, they will not reproduce at all. However, selection is likely to be stronger on parasites because every brood parasite must successfully parasitize its host in order to reproduce (Dawkins and Krebs 1979). By contrast, only a few individuals in the host population will be parasitized at any moment in time, and most hosts will breed at least once without being parasitized—although see Hauber (2001) and Molina-Morales et al. (2013). This asymmetry in costs between parasites and hosts could potentially lead to stronger selection in parasites (at least initially) to evolve strategies to exploit their hosts and to diversify morphologically. In the next sections, we will show evidence of the effects of brood parasitism in both the exploiters and the victims at micro- and macroevolutionary levels.

Phenotypic diversity in brood parasites

Obligate avian brood parasites depend exclusively on their hosts to reproduce, and there is evidence that this behavior may have evolved after a transition to lower productivity habitats, which also resulted in a reduced brain size that diminished energetic demands (Boerner and Krüger 2008). Obligate brood parasitism has evolved independently in 7 lineages of birds (Figure 2): parasitic cuckoos (3 times, Cuculidae, 58 spp.), which have a worldwide distribution and constitute the largest radiation, honeyguides (Indicatoridae, 17 spp.) and Vidua finches (Viduidae, 20 spp.), which are exclusively African, and cowbirds (*Molothrus* spp., 6 spp.) and one species of duck *Heteronetta atricapilla*, which occurs in the Americas (Payne 2005a).

The obligate parasitic lifestyle has led to changes and adaptations in a variety of traits (reviewed in Davies 2011). For instance, the absence of costly parental care in brood parasites is predicted to lead to more plastic mating systems, higher male promiscuity, and sexually selected traits, compared with species that provide parental care, and brown-headed cowbirds *M. ater* conform to this expectation (Louder et al. 2019). It was also recently found that brood parasitic cuckoos have a higher degree of dietary specialization compared with nonparasitic cuckoos, although the mechanisms behind this association are unknown (Morelli et al. 2020). In contrast to closely-related species that are not parasites, many avian brood parasites also have smaller eggs and smaller body sizes (Krüger and Davies 2002), traits that are thought to be adaptations for parasitizing smaller hosts that lay smaller eggs. Some brood parasites also have thicker eggshells (Brooker and Brooker 1991), which can protect the parasitic egg from damage by hosts or other parasites. It has also been found that parasitic cuckoos have less complex and lower frequency vocalizations, which might travel better through their large breeding rages (Kim et al. 2017). Additionally, the existence of cuckoo–hawk mimicry (Davies and Welbergen 2008) has led to parasitic cuckoos being more likely to have barred plumages compared with nonparasitic species (Krüger et al. 2007). All these morphological adaptations suggest that the transition to brood parasitism has increased avian phenotypic diversity between clades, because the parasitic lifestyle has generated phenotypic differences between closely-related parasitic and nonparasitic clades, which are otherwise unlikely to have emerged.

A parasitic lifestyle has also selected for the evolution of diverse strategies to exploit hosts, which can be accompanied by morphological adaptations. For instance, honeyguides (*Indicator* spp.) and striped cuckoos *Tapera naevia* kill all the progeny of their host and are thus considered highly virulent parasites—sensu Kilner (2005). To achieve this, chicks have evolved hooks at the end of their bills that are used to stab the host’s progeny (Morton and Farabaugh 1979; Spottiswoode and Koorevaar 2011). Other cuckoo chicks (subfamily Cuculinae) get rid of their competition for food by balancing the eggs of the host on their backs and evicting them from the nest (Brooker and Brooker 1989a). The broad, concave back of cuckoo nestlings is believed to be an adaptation for balancing host eggs on their backs (Davies 2000). By contrast, chicks of *Vidua* finches and cowbirds can be raised alongside host progeny (Kilner 2005), so they lack morphological adaptations for eliminating the progeny of the host directly—although they can have behavioral adaptations to be more competitive than the host progeny (Kilner 2003; Soler and Soler 1991).

Differences in the costs of parasitism to hosts (virulence) may affect the likelihood of macroevolutionary consequences. From a theoretical perspective, mutualistic interactions—where both participants

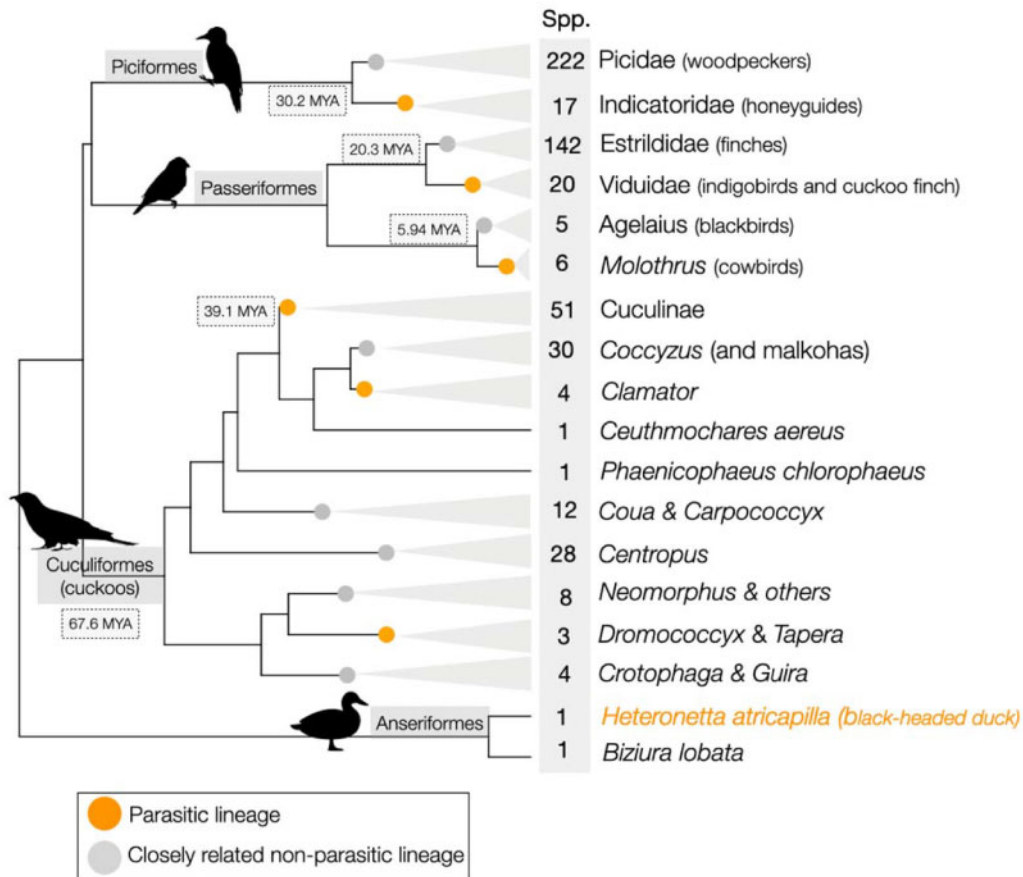


Figure 2. Phylogenetic relationships between parasitic clades. For reference, parasitic clades (orange) are presented along with their more closely-related non-parasitic lineage (gray). Points represent the most recent common ancestor for all the members in that clade. We present some ages as a reference, to demonstrate that some parasitic lineages such as Cuculinae and Indicatoridae diverged longer ago compared with *Vidua* finches or cowbirds. Silhouettes from phylopic.org. Tree reconstruction performed using birdtree.org (Jetz et al. 2012).

benefit—are much less likely to lead to diversification than parasitic interactions (Yoder and Nuismer 2010). Consideration of these differences is important in understanding the role of brood parasitism in diversification processes. For example, an almost mutualistic relationship has evolved between the great spotted cuckoo *Clamator glandarius* and its host, the carrion crow *Corvus corone*; cuckoo chicks produce repellent secretions that can decrease predation rates (Canestrari et al. 2014). If predation rates are high, then raising a cuckoo can be beneficial for crow chicks. In such case, trait modification in the cuckoo as a result of its parasitic lifestyle is less likely, because hosts are unlikely to evolve defenses against the parasite that brings them fitness benefits.

Phenotypic variation within parasitic species

Arguably the main source of selection on phenotypic variation in brood parasites is on traits that circumvent host defenses. One of the best documented defenses in hosts of brood parasites is egg rejection, and there are dozens of species that are known to evict parasitic eggs based on their phenotype (Soler 2014). As explained above, egg rejection by hosts has selected for brood parasite eggs that mimic those of their respective hosts in size (Krüger and Davies 2004), shape (Zölei et al. 2012; Attard et al. 2017), color (Avilés et al. 2006; Spottiswoode and Stevens 2012), and pattern (Stoddard

and Stevens 2011). The correlated evolution of egg rejection by hosts and egg mimicry by parasites is one of the best examples of a coevolutionary arms race in nature (Rothstein 1978; Kelly 1987; Edvardson et al. 2001; Langmore et al. 2003; Avilés et al. 2004; Starling et al. 2006; Spottiswoode and Stevens 2010; Stoddard and Stevens 2010). Mimicry (in color, pattern, or size) between hosts and parasites can lead to a higher diversity of egg phenotypes within parasitic species that exploit multiple host species, as each gens (host-specific race) matches the egg phenotype of their own host. This has been shown in several generalist parasitic species, where cuckoo eggs and cuckoo finch eggs mimic the eggs of different hosts and are highly variable within-parasitic species (i.e., among gentes; Moksnes and Røskaft 1995; Starling et al. 2006; Stoddard and Stevens 2010; Spottiswoode and Stevens 2011; Spottiswoode et al. 2011).

The interaction between hosts and parasites has led not only to egg mimicry but also to mimicry of host chicks by brood parasites (Grim 2011; Langmore et al. 2011). Selection due to chick ejection by hosts can lead to chick mimicry, but mimicry can also evolve due to provisioning rules used by host parents when responding to begging calls from their progeny, or due to direct competition with host nestlings for care from host parents (Davies et al. 1998; Hauber and Kilner 2007). Although less common than egg mimicry, there are

multiple examples of cuckoo species that mimic the nestlings or fledglings of their hosts (Sato et al. 2010; Langmore et al. 2011; de Marsico et al. 2012; Sato et al. 2015). Selection for mimicry of host chicks has led to diversity in cuckoo nestling traits within species, such as the color of the skin, rictal flange and gape and the number of nestling down feathers (Langmore et al. 2011; Langmore and Spottiswoode 2012) and begging calls (Langmore et al. 2008). Just as the coevolutionary arms race, and specifically rejection by host parents, can increase within-species variation in the eggs of parasites (polymorphisms), there is also evidence of diversification in chick morphology within species of parasites. For example, the shining bronze-cuckoo *C. lucidus* is suggested to mimic the chicks of the fan-tailed gerygone *Gerygone flavolateralis* in New Caledonia. Furthermore, host nestlings exist in different color morphs, which are matched by equivalent color morphs in the cuckoo's nestlings (Sato et al. 2015). These polymorphisms might be the result of the coevolutionary dynamics described above by Yoder and Nuismer (2010), though this interpretation has yet to be tested experimentally.

In the case of chick and egg mimicry, there is potential for genetic divergence in phenotype between populations parasitizing different hosts (as is the case in the examples above). In other traits, however, adaptations to match the phenotype of different hosts do not have to necessarily lead to evolutionary divergence, but can instead arise through phenotypic plasticity. Horsfield's bronze-cuckoo chicks mimic the begging calls of their different hosts, but cross-fostering experiments show that individual chicks can mimic the different call types produced by their different hosts depending on which host nest they are in (Langmore et al. 2008). Such plasticity is likely to hinder genetic divergence and the formation of races, genets, or subspecies in this parasite (contrary to what occurs with variation in egg or chick phenotype; Langmore et al. 2008).

Besides egg and chick rejection, many host species have also evolved frontline defenses, such as mobbing, which prevent parasitism before egg laying. Several species of passerines are known to recognize and attack their brood parasites (Feeney et al. 2012; Glog et al. 2013; Medina and Langmore 2016a) and this response can be highly plastic and respond to local parasitism rates (Welbergen and Davies 2009). Mobbing and parasite recognition have led to the evolution of hawk-like traits in cuckoos (such as barred chest or yellow legs) to intimidate their hosts (Davies and Welbergen 2008), or the evolution of plumage that resembles local nonaggressive models to avoid detection (Feeney et al. 2015). Thorogood and Davies (2013) showed that this counteradaptation against mobbing (hawk-like mimicry) is associated with higher phenotypic diversity within species of parasites, because there is potential for plumage divergence due to mimicry of different local models. Hence, cuckoo species with hawk-like plumage are more likely to be polymorphic than cuckoo species that do not look like hawks. Moreover, Hasegawa and Arai (2018) recently found that differences in plumage color between juvenile and adult life stages are larger in brood parasitic species than in species with parental care, which could have resulted from different sources of selection acting on phenotype at different life stages (i.e., selection from foster parents in juveniles and sexual selection in adults). This last example represents another dimension of phenotypic diversity that can be exacerbated by brood parasitism: variation within individuals, across different life stages.

Phenotypic variation in brood parasites above the species level

In general, different brood parasitic species exploit different hosts. Some brood parasitic species are generalist and other species are

specialists, but there is little overlap in the main host species being exploited by sympatric parasitic species (Medina and Langmore 2016b). If different brood parasitic species exploit different host species, and each parasite responds to pressures imposed by its own host, then this might drive increased phenotypic diversity in parasitic clades, as species diverge to better exploit their victims. Phenotype matching of hosts by parasites—such as the evolution of smaller egg sizes to match the phenotypes of their hosts—or the evolution of plumage to match local antagonistic models (hawk mimicry) increases the potential for the evolution of phenotypic variation between parasitic species (Yoder and Nuismer 2010). Medina and Langmore (2015a) showed that rates of phenotypic evolution are in fact higher in parasitic cuckoos than in nonparasitic cuckoos and other brood parasites. Both egg size and a component of plumage associated with hawk-mimicry evolve faster in parasitic cuckoos, suggesting that brood parasitism can lead to increased phenotypic diversity in the exploiters. Interestingly, the higher rate of hawk-like plumage evolution in parasitic cuckoos corresponds nicely with the work of Thorogood and Davies (2013) that we mentioned before; parasitic species of cuckoos with hawk-like plumage tend to be polymorphic and parasitic cuckoos tend to rapidly evolve differences in hawk-like plumage among species. Both findings strongly suggest that mimicry due to a parasitic lifestyle can lead to phenotypic diversification in plumage within and among species.

Notably, cuckoos seem to be the only lineage where brood parasitic behavior is linked to increased phenotypic diversity at a broad scale (across species). Neither honeyguides nor *Vidua* finches show a similar association and in fact honeyguides seem to have slower rates of phenotypic evolution compared with their sister clade, woodpeckers (Medina and Langmore 2015a). This is not totally unexpected, given the differences in the degree of relatedness to their hosts, the differences in virulence between the 3 lineages and the age of the interactions. Brood parasites that are more distantly related to their hosts are likely to undergo greater phenotypic changes in response to selection for mimicry of host attributes, because they are more morphologically different to begin with, so mimicry is likely to require more dramatic alterations to the body plan (Pekar and Jarab 2011). Moreover, the more virulent parasite lineages (such as cuckoos and honeyguides) select for stronger host defenses (Medina and Langmore 2015b; Soler and Soler 2017), which in turn select for a greater diversity and refinement of counteradaptations on the part of the parasite. Finally, in the older lineages of brood parasites, there has been more time for the evolutionary arms race with hosts to play out, leading to a greater diversity and sophistication of adaptations and counteradaptations in hosts and parasites. Cuckoos mostly parasitize hosts from a different order, and constitute the oldest radiation of brood parasites (~65 MYA; Sorenson et al. 2003). Honeyguides also parasitize very distantly-related hosts, including passerines and bee-eaters, but they are a much younger lineage (~20 MYA; Sorenson et al. 2003). On the other hand, *Vidua* finches are less virulent than both cuckoos and honeyguides, and they are very young clade (~2.5 MYA; Sorenson et al. 2003) that parasitizes hosts from their sister family, Estrildidae. Therefore, it is not unexpected that *Vidua* finches do not show any signal of an increase in rates of phenotypic evolution—although see discussion on mouth markings below (Payne 2005b). Not all coevolutionary interactions are likely to lead to increased diversity, and even within types of interactions, differences in parameters such as the strength of selection can determine the likelihood of diversification.

Following the logic of the studies on egg size and plumage, we would expect parasitic lineages to have higher rates of phenotypic

evolution of egg coloration compared with nonparasitic lineages. Kilner (2006b) showed that brood parasites have higher variation in egg appearance between species compared with nonbrood parasites, which support this idea. It would be interesting to test whether this increased variation among species is echoed by higher evolutionary rates. At the chick stage, there are no studies to our knowledge that test whether chick rejection and mimicry could have macroevolutionary effects (i.e., lead to higher chick variation between species of parasites vs. nonparasites) and chicks tend to have low phenotypic variation in skin color in general (Kilner 2006a). There is, however, extensive variation in nestling mouth markings in parasitic *Vidua* finches among species, which is suggested to be an adaptation to match the markings of different host species (Payne 2005b). Payne (2005b) acknowledges that it is difficult to know whether host-parasite coevolution is the main force responsible for the high diversity of mouth markings in this group of parasites and hosts. This is partly because there is a high diversity of mouth markings even in species unconnected to brood parasitism within this clade (Viduidae and Estrildidae). In addition, there is no conclusive evidence that host parents discriminate against nestlings based on their mouth markings. Consequently, is it possible that hosts are actually mimicking the parasites, rather than the parasites mimicking their hosts (Hauber and Kilner 2007; De Mårsico et al. 2017, pp. 557–574).

Diversification in cuckoo nestling traits does occur close to the species level, though (Langmore and Spottiswoode 2012). Subspecies of cuckoos that exploit different hosts also have chicks that differ from one another in some traits and resemble their respective hosts in these traits (Langmore and Spottiswoode 2012). A study by Ranjard et al. (2010) found that the begging calls of a cuckoo subspecies in New Zealand have diverged significantly from the continental species begging call of *C. lucidus*, possibly because they exploit a different host. Future studies could explore whether there is greater evolutionary lability specifically in the traits that are matched between parasites and their host (where species and subspecies mimic their hosts) or whether there is simply greater trait lability in general in these species. It would also be interesting to investigate whether chick (and even adult) coloration and begging calls evolve faster in parasitic clades that exhibit mimicry of nestling phenotypes.

Evolution of phenotypic diversity in hosts

Hosts of avian brood parasites suffer very high costs from being parasitized. They invest time and energy feeding a chick that is not their own and, in many cases, also lose all their progeny (Davies 2000). More than 500 species of passerines are main hosts of brood parasites, plus some woodpecker, bee-eater, and waterbird species (Friedmann 1949; Friedmann and Kiff 1985; Brooker and Brooker 1989b). Antagonistic interactions with phenotypic matching (such as in brood parasites) should lead to phenotypic diversity not only in parasites, as we saw in the previous section, but also in host species. This is expected because, to circumvent the counteradaptations in parasites (e.g., mimicry), the host phenotype should evolve away from the parasitic phenotype, or there should be selection for increased variability in the host population to reduce the chance of matching the phenotype of the parasite (Takasu 2003). In a microcosm experiment in bacteria, Buckling and Rainey (2002) showed that the diversity between isolated populations of *Pseudomonas fluorescens* was higher in communities with parasites, because *P. fluorescens* populations followed divergent evolutionary trajectories to resist the parasite, resulting in increased diversity. In hosts of brood

parasites increased diversity at macroevolutionary scales is accordingly also expected. However, this is a much harder issue to test.

Hosts are taxonomically widespread; it is not common to have whole clades of hosts and nonhosts, and it is actually not that simple to confidently classify a species as a nonhost. Many species have not been studied sufficiently. There can also be geographic variation in preferred hosts, as well as instances of host-switching (Payne et al. 2002; Sorenson et al. 2003). Moreover, there is no way of having certainty about the duration—and thus the evolutionary effects—of some of these interactions. Additionally, the fact that hosts are distributed across many different clades in the phylogeny can make calculations of evolutionary rates complicated, because they are usually calculated for whole clades (i.e., parasitic vs. nonparasitic cuckoos), rather than particular species (although see Rabosky 2014). All these reasons make assessment of evolutionary rates in hosts, and appropriate comparisons across species, much more complicated.

Host diversity within and among species in relation to phenotype-matching

As discussed earlier, one of the main defenses in hosts is rejection of brood parasitic eggs. Hosts that are small relative to the parasite and are exploited by a highly virulent parasite, are more likely to express egg rejection behavior (Medina and Langmore 2015b)—but see Table 1 in Kilner (2003). The capacity to reject eggs can be highly variable not only among species but also within species, within populations through time, and between populations of the same species (Briskie et al. 1992; Soler et al. 1999; Liang et al. 2016). In some cases, such as in American robins *Turdus migratorius* or gray catbirds *Dumetella carolinensis*, this behavior is genetically determined (Peer et al. 2011; Kuehn et al. 2014) but in other species egg rejection responses are product of phenotypic plasticity (Lindholm 2000; Lahti 2006; Ruiz-Raya and Soler 2017, pp. 449–471). The existence of phenotypic plasticity in egg rejection behavior in some species means that this defense is not necessarily costly and can be retained cryptically in the absence of parasitism (Lahti 2005). Phenotypic plasticity could thus retain “ghosts of counter-adaptations past” within lineages, which would otherwise be lost if selective pressures are relaxed (Lahti 2005).

As explained above, egg rejection behaviors have led to the evolution of egg mimicry by brood parasites, and this arms race has in turn selected for variation in egg phenotype, both within and among host species (Soler and Møller 1995; Landstrom et al. 2010; Spottiswoode and Stevens 2011). Theory suggests that hosts should evolve high variation in egg phenotype between individuals of the same population, because it would be harder for the parasite to mimic different types of eggs (Øien et al. 1995; Soler and Møller 1995). This microevolutionary prediction has been supported by many studies, where it has been shown that host species tend to have individual egg signatures, to facilitate recognition of their own eggs (Stoddard et al. 2014; Caves et al. 2015). A study of the cuckoo finch *Anomalospiza imberbis* and its host prinia *Prinia subflava* showed that the variation in egg color of both host and parasite eggs increased significantly over a 40-year period, with a shift toward more extreme and diverse colors in the host that was closely tracked by the parasite (Spottiswoode and Stevens 2012). Furthermore, within-population variation in egg patterns is higher in parasitized populations than in nonparasitized populations of the same species, suggesting that parasitism has indeed led to higher variation in egg pattern across host individuals (Caves et al. 2017).

Table 1. Summary of examples cited in Figure 3

Ref #	Category	Level of variation	Trait	Reference
1	Parasites	Within species	Egg colour and pattern	Moksnes and Røskaft (1995)
2	Parasites	Within species	Egg colour and pattern	Stoddard and Stevens (2010)
3	Parasites	Within species	Egg colour and pattern	Spottiswoode and Stevens (2011)
4	Parasites	Within species	Egg colour and pattern	Starling et al. (2006)
5	Parasites	Within species	Egg size and shape	Spottiswoode et al. (2011)
6	Parasites	Within species	Chick colour	Sato et al. (2015)
7	Parasites	Within species	Adult plumage	Thorogood and Davies (2013)
8	Parasites	Between species	Egg size and hawk-like plumage	Medina and Langmore (2015a)
9	Parasites	Parasites vs. nonparasites	Smaller egg and body size	Krüger and Davies (2002)
10	Parasites	Parasites vs. nonparasites	Higher eggshell thickness	Brooker and Brooker (1991)
11	Parasites	Parasites vs. nonparasites	Hawk mimicry	Davies and Welbergen (2008)
12	Parasites	Parasites vs. nonparasites	Less vocal complexity	Kim et al. (2017)
13	Parasites	Parasites vs. nonparasites	Smaller brains, but could have evolved before parasitism.	Boerner and Krüger (2008)
14	Hosts	Within species	Egg colour and pattern	Soler and Møller (1995)
15	Hosts	Within species	Egg colour and pattern	Landstrom et al. (2010)
16	Hosts	Within species	Egg colour and pattern	Stoddard et al. (2014)
17	Hosts	Within species	Egg colour and pattern	Caves et al. (2015)
18	Hosts	Within species	Egg colour and pattern	Spottiswoode and Stevens (2012)
19	Hosts	Within species	Chick colour	Sato et al. (2015)
20	Hosts	Between species	Egg colour and pattern	Medina et al. (2016)
21	Hosts	Hosts vs. nonhosts	Smaller clutch size in cowbird hosts	Hauber (2003)
22	Hosts	Hosts vs. nonhosts	Lower fledgling mass in hosts	Remeš (2006)
23	Hosts	Hosts vs. nonhosts	Smaller clutch size and more breeding attempts in hosts	Avilés (2019)
24	Hosts	Hosts vs. nonhosts	More breeding attempts in hosts	Hauber (2003)
25	Hosts	Hosts vs. nonhosts	More likely to breed cooperatively	Feeney et al. (2013)
26	Hosts	Hosts vs. nonhosts	Thicker eggshells	Spottiswoode and Colebrook-Robjent (2007)

At a broader scale, it has also been shown in Australia that host species of brood parasites have diverged more from each other in their egg pattern than those species that are nonhosts, after controlling for divergence time (Medina et al. 2016). This evidence suggests that the egg phenotype of each species of host is evolving in response to parasites along a different evolutionary trajectory, leading to divergence between species. Different evolutionary trajectories could arise even if species are subject to similar pressures, because pre-existing genetic variation in egg color and pattern within each species might make some evolutionary paths more likely than others.

As mentioned earlier the arms race between hosts and parasites has escalated to the chick stage. Template-based recognition in the large-billed gerygone *G. magnirostris*, in which hosts can recognize their own chicks based on the density of nestling down-feathers, has selected for mimicry of host chicks by cuckoos (Noh et al. 2018). It is possible that it has also caused the evolution of host chick polymorphism within species (see above), which is rare in birds (Sato et al. 2015). It is also possible that antagonistic coevolution has generated greater levels of variation among host species too. The mouth markings in Estrildid finches vary more among hosts of *Vidua* brood parasites, than among nonhost species (Payne 2005b). However, these greater measures of diversity are confined only to some aspects of the mouth markings: there is no difference in the diversity of melanin markings or gape structures between hosts and nonhosts, which are considered key elements in this signal (Payne 2005b). Further work is needed to test whether brood parasitism generally leads to higher diversity of host chick phenotypes across species.

Host diversity among species in relation to other traits

The selective pressures from brood parasites on hosts also appear to have diversified traits that are not directly involved phenotype matching, at least in comparisons of clades that are parasitized with those that are not. For example, parasitism by cowbirds in America may have contributed to variation in clutch size (and number of breeding attempts) (Hauber 2003). Old hosts of these brood parasites have a smaller clutch size compared with nonhost species or new hosts, perhaps as part of an evolved strategy of tolerating brood parasites rather than rejecting them (Hauber 2003). In Europe, hosts of cuckoos have not evolved smaller clutches than nonhosts (Medina et al. 2017; Avilés 2019) because they mount defenses against brood parasites rather than tolerating. Strategies of tolerance are more likely to evolve when parasitism is less costly, as for hosts of nonevicting parasites (like cowbirds) whereas host defenses are more likely to evolve in response to costly parasitism by evicting parasites like cuckoos. Thus the extent of virulence shown by the brood parasite contributes to the extent of diversification in host traits that are not connected with phenotype-matching.

Besides clutch size, at least some of the variation in growth rates of passerines can be explained by brood parasitism: Remeš (2006) showed that host species have lower fledgling mass and shorter nestling periods compared with nestlings of closely-related nonhost species. Furthermore, in honeyguides, eggshell thickness in different species is correlated with the risk of parasitism and the risk of exposure to egg puncturing behavior from the parasite (Spottiswoode and Colebrook-Robjent 2007).

The interactions between hosts and parasites are further associated with the diversity of behavioral phenotypes among host species. There is evidence of vocal diversification in hosts in response to brood parasitism, because some host species produce brood parasite-specific alarm or mobbing calls (Gill and Sealy 2004; Langmore et al. 2012; Feeney and Langmore 2013). Species that are hosts of brood parasites in Africa and Australia are also more likely to be cooperative breeders than species that are nonhosts (Feeney et al. 2013). Hosts that exhibit cooperative breeding may gain a benefit if larger groups can defend their nests better from brood parasites than a pair. Conversely, brood parasites may also benefit by exploiting cooperatively breeding species, because there are more individuals to provision their young. There is evidence from one species, the superb fairywren *Malurus cyaneus*, that helpers at the nest strengthen host defenses and lead to lower parasitism rates (Feeney et al. 2013). Whether brood parasitism leads to cooperative breeding, or vice versa is difficult to determine (Feeney et al. 2013). Either way, brood parasitism is linked with differences in host breeding systems.

Similarly, the density of host nests is likely to affect the probability of brood parasitism, though in complex ways. At one extreme, colonial nesters can combine forces to defend their nests, whereas at the other extreme species with very sparsely distributed nests may offer insufficient host nests available to support breeding by brood parasites. Populations with nests at intermediate densities are thus predicted to be associated more frequently with brood parasites. This prediction is supported both within and among species; in populations of superb fairywrens, the probability of parasitism increases when populations are at intermediate density (Medina and Langmore 2019). At broader scale, species that are hosts of brood parasites are more likely to have intermediate-sized territories (Medina and Langmore 2019), when compared with nonhost species. However, whether or not host breeding density is an evolved response to brood parasitism is hard to determine. An alternative

scenario is that parasites target hosts that nest at intermediate densities because they offer sufficient nests to support a clutch of brood parasitic eggs, but are not so scattered that they are hard for brood parasitic females to locate or defend.

One topic that we have not covered in this review is the effect of brood parasitism on speciation. Speciation is the result of restricted gene flow between populations. The associated reproductive isolation of populations can lead to further genetic divergence, and hence increased phenotypic diversity, as a by-product of the genetic differentiation. There is some evidence that brood parasites have high speciation rates, at least in *Vidua* finches where rapid sympatric speciation has occurred as a result of host-switch (Sorenson et al. 2003). Parasitic males mimic the song of their hosts and females use these songs to choose their mates, generating reproductive isolation between populations that exploit different hosts. Rapid speciation rates in *Vidua* finches, however, do not seem to be linked with higher rates of phenotypic evolution in this clade, at least in traits like egg size and adult plumage. In honeyguides, there is no evidence of a link between brood parasitism and speciation, and in cuckoos the available evidence is not conclusive (Krüger et al. 2009; Medina and Langmore 2015a). There is no evidence, therefore, that brood parasitism in general accelerates speciation rates.

Conclusions and Future Directions

The studies cited in this review provide evidence that natural selection exerted by brood parasites on hosts has important effects in the generation of phenotypic diversity at different scales (Figure 2). Within species, selection to reach and escape phenotype matching (on parasites and hosts respectively) has led to polymorphisms in eggs and chicks, in both the exploiters and the victims. We provide evidence of the intensive research focus on phenotypic variation in different traits that have been studied within and among populations of the same species (Figure 3). Our survey also reveals that selection



Level of variation	In parasites 			In hosts 	
Within species	Egg colour pattern [1-4]	Chick skin colour [6]	Adult plumage [7]	Egg colour pattern (signatures) [14-18]	Chick skin colour [19]
Between species within category	Egg size [5]		Adult plumage [8]	Egg colour pattern [20]	
Between categories (host vs non-host/ parasite vs non-parasite)	Egg size ↓ [9]	↑ Hawk-like plumage [11]	↓ Vocal complexity [12]	↓ Clutch size [21,23]	↑ Breeding attempts [23,24]
	↑ Eggshell thickness [10]	↓ Brain size [13]		↑ Eggshell thickness [26]	↑ Cooperative Breeding [25]
				↓ Fledgling mass [22]	

Figure 3. Graphic summary of evidence of brood parasitism as a driver of phenotypic variation at different scales: variation within species (e.g., among individuals, populations, genets), variation between species within category (e.g., among host species or parasitic species), variation between clades (e.g., between parasitic and nonparasitic clades, or host and nonhost species). For examples of variation between categories, we place arrows indicating the direction of the change (i.e., decrease in egg size in parasites, increase in breeding attempts in hosts). Numbers below different traits indicate the relevant references, which can be found in Table 1.

on parasites to exploit hosts more efficiently, and on hosts to defend themselves from parasites, has led to phenotypic differences between avian clades. A wide variety of traits has been identified as statistically different between hosts and nonhosts, and parasites and nonparasites (Figure 3).

Evidence that brood parasitism drives phenotypic variation at an intermediate level, namely *between* species, is scarce. Few studies have tested explicitly whether coevolution can and has led to higher phenotypic variation between closely-related species of both parasites and hosts. The studies available suggest that if different host–parasite systems follow different evolutionary paths, as a result of the arms race, then phenotypic divergence between species can arise and cause higher rates of phenotypic evolution for the clade as a whole. The development of novel macroevolutionary techniques to quantify evolutionary rates like BAMM or RRPhylo (Rabosky 2014; Castiglione et al. 2018) and global phenotypic datasets will allow further exploration of this topic. It may be phenotypic variation between species is seldom due to coevolution between hosts and brood parasites. Recent phylogenetic methods such as phylogenetic path analyses (e.g., phylopath; van der Bijl 2018) and phylogenetic linear mixed models (e.g., MCMCglmm and BRMS; Hadfield 2010; Bürkner 2017) offer much greater flexibility in testing hypotheses regarding the origin of phenotypic variation among species of both hosts and parasites, and could fruitfully be employed in future work.

There is still room for future studies assessing the impact of brood parasitism in the evolution of phenotypic divergence. This study identified several traits where variation has been studied at the population (within species) level but not more broadly than that. For instance, it is currently unknown whether egg color pattern in parasitic lineages has evolved higher rates of phenotypic evolution than in nonparasitic lineages. Furthermore, although there is less broad-scale information on nestling morphology, it would also be interesting to investigate whether parasitic and host species—in systems which chick mimicry—have higher rates of skin color evolution compared with systems with no chick mimicry, and compared with nonparasites and nonhosts.

Another insight from our literature review is that evidence of variation in parasite traits is more common than for host traits (Figure 3). This could be due to the fact that selective pressures are stronger on parasites to successfully parasitize—the life-dinner principle mentioned in at the beginning of “The Study System: Avian Brood Parasitism” section. However, it could also be due to the fact that fewer studies have focused on host diversity. Comparisons of hosts and nonhosts are statistically more difficult, because hosts are widespread across the avian tree and comparing species with different and varied evolutionary histories requires more statistical power. Consequently, it is too soon to conclude that parasites are under stronger pressures than hosts to evolve adaptations and consequently express greater phenotypic variation.

To our knowledge, there are no explicit tests that compare rates of phenotypic evolution between brood parasites and hosts. One system that offers a good opportunity to test this is the interaction between *Vidua* finches and their hosts, because their hosts are not only mostly contained in one clade (Estrilidae) but this clade is also the sister clade of the *Vidua* family, Viduidae. Evidence so far suggests that some traits (egg size, body size, and plumage) have not evolved differently in the parasitic and the host clade (Medina and Langmore 2015a), although *Vidua* finches have some of the highest speciation rates in passerines, which is not the case for finches (Sorenson et al. 2003; Harvey et al. 2017).

One trait that has been largely ignored in studies of hosts and parasites, and which is part of the host’s extended phenotype, is its nest. In weaver nests, a long entrance tube is suggested to hinder the entrance of the diederik cuckoo *Chrysococcyx caprius* (Freeman 1988). Adaptations of nests could be useful as a frontline defense, and present broadscale variation due to parasitism. Presumably, species with larger nests will be more easily detected than species with smaller nests, and having a very small nest could make egg laying more difficult for a brood parasite given their relatively larger size. Likewise, particular nest traits could also evolve in response to parasitism pressures. Many species with domed nests have small entrances covered by a hood. The presence of this hood might decrease both probability of nestling and egg predation and parasitism. Therefore, we would expect an association between nest trait diversity and the frequency of parasitism.

A final possibility for future work is variation that results from differences in the intensity of parasitism between populations. Such differences could lead to a geographic mosaic of coevolution, a topic that has been mostly explored in insect coevolutionary systems (Thompson 2005; Lorenzi and Thompson 2011). In a review on host–parasite and plant–herbivore systems, Laine (2009) showed that in 100% of the studies, geographic variation in the strength of the interaction has led to the evolution of genetic and phenotypic diversity in host plants. In the case of brood parasites, host populations of the same species that vary in parasitism rates and defenses might also evolve genetic and phenotypic differences, in addition to the observed differences in defenses. There is evidence that both parasitism rates and defense levels (i.e., egg rejection) can vary across populations (Briskie et al. 1992; Soler et al. 2011), but it is unclear whether these differences in defenses might also result in differences in egg phenotypes between populations. If egg rejection rates vary across populations, for example, this could lead to the evolution of mimicry in some populations and not others (or to differences in the accuracy of mimicry). This in turn, could lead to high levels of variation in egg phenotype within host species, that is, independent of the variation generated by the host in trying to escape egg mimicry by its parasite. This possibility has received little attention to date and would be an interesting avenue to explore further.

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Conflict of Interest

The authors declare no conflict of interest.

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