Polymorphism in Avian Brood Parasitism: A Coevolutionary Perspective

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Abstract
Polymorphism provides a classic example of adaptive evolution. A great advantage of studying polymorphism is that the phenotype can serve as a genetic marker; therefore, researchers can take full advantage of this to test a hypothesis based on Darwin’s principle of adaptive evolution. Evolutionary theories of polymorphism have been established and suggest that polymorphism is likely maintained through negative frequency-dependent selection. Such selection is mediated by the viewer’s perception or recognition of the focal trait as expressed by appearance, such as the colour and pattern of eggs. The viewer’s response to that trait selects against the majority of the population, and thus favours the rare type. Such evolutionary dynamics can also be applied to avian brood parasitism, in which parasites exploit the parental care of their hosts. In this review, I describe recent findings in brood parasitic systems, in which polymorphism plays an important role in the coevolutionary arms races, at the egg, chick, and adult stages. Finally, I emphasize the need to synthesize traditional ultimate approaches with proximate approaches, incorporating genomics and psychology, in order to draw a fuller picture of the coevolutionary arms race between avian brood parasites and their hosts.

Key words Brood parasitism, Coevolutionary arms race, Polymorphism, Proximate and ultimate causes, Recognition and perception

Evolutionary Theory of Polymorphism
Initially, I will define polymorphism, then describe several existing theories that have attempted to explain its evolution. When multiple phenotypes of a trait coexist within a single breeding population, the species concerned is defined as polymorphic; a classic example involves the typical pale morph and the dark, melanistic morph of the Peppered Moth (Darwin 1869). In recent years, accumulated evidence has shown that polymorphism among avian brood parasites plays an important role in their coevolutionary arms races with their hosts. In this review, I first describe the underlying evolutionary theories explaining polymorphism. Then, I review recent trends in brood parasitism studies in terms of polymorphism, and finally I propose future directions for research in order to comprehensively unravel the nature of avian brood parasitism.
tages allow several morphs to persist through adaptive evolution.

The advantages experienced by each morph alone are insufficient for polymorphism to exist, because such heterogeneity in the advantage would likely lead to speciation through local adaptation (van Doorn et al. 2009). The different advantages that the respective morphs experience mean that either of the morphs is suboptimal in a particular situation, and thus would be locally selected against. Therefore, for polymorphism to evolve and to be maintained in a population, dependence of the advantage of each morph on the other(s) is essential. One such example involves “sneaker” males among certain salmon (e.g., Coho Salmon Oncorhynchus kisutch). Sneaker males can attain sexual maturity more rapidly than fully mature “hooknose” males. Their smaller size means that sneaker males are disadvantaged during physical combat with hooknosed males, but, that same small size allows them to insinuate into the spawning sites of hooknosed males, and successfully fertilize some of the eggs released by the hooknosed males’ mates. This size polymorphism among male salmon is traditionally regarded as an alternative, evolutionary stable strategy (ESS; Gross 1985) in mating. Furthermore, the fitness advantage of sneakers is dependent on the existence of hooknosed males, and thus cannot exist alone.

In contrast to evolutionary stable polymorphic strategies, in some cases the dependent fitness advantages of polymorphism are not dynamically stable. In such cases (defined as negative frequency-dependent selection) the advantage of the few, namely, the minority in the population is favoured, while selection acts against the majority in that same population. Negative frequency-dependent selection can cause a temporal transition between the fitness advantage of one trait and that of another. In such species, the frequency of morphs in a population is expected to oscillate over time (Clarke 1964; Takahashi & Hori 1994). What is important here is that, if the focal polymorphism is in the appearance of the organism, then the cognitive or perceptive ability of the viewer is substantially involved in the evolutionary maintenance of polymorphism. This is maintained through negative frequency-dependent selection, by means of search image or vigilance, and is known as apostatic selection (Allen & Clarke 1968). For example, discrete dichromatism is maintained in flowers of a deceptive orchid Dactylorhiza sambucina that does not provide pollinators with a nectar reward; each morph alternately becomes the majority (Gigord et al. 2001). Cheated pollinators visit flowers of the rare type frequently enough to enhance the reproductive success of the rare type, because the pollinators have few chances to learn its floral colour to avoid. Such temporal oscillation in morph frequency, mediated by viewer perception or recognition is also found in the handedness of a scale-eating cichlid Perissodus microlepis and its prey (Hori 1993; Takahashi & Hori 1994), in male-mimicking females of a damselfly Ischnura senegalensis (Takahashi et al. 2010), as well as in typical and melanic morphs of the Peppered Moth (Cook et al. 2012).

In the coevolutionary arms race between avian brood parasites and their hosts, the host’s ability to recognize and reject brood parasites is known as the fundamental drive. Therefore, polymorphism among brood parasites is also expected to be a consequence of the coevolutionary arms race through apostatic selection.

Polymorphism in Avian Brood Parasitic Systems

Here I review recent studies highlighting egg, chick, and adult polymorphism found in brood parasitic systems.

Egg polymorphism

A classic example of polymorphism in relation to brood parasitism is the between-nest (inter-clutch) variation in the appearance of the eggs of the Reed Warbler Acrocephalus scirpaceus parasitized by the Common Cuckoo Cuculus canorus. Such inter-clutch variation is favoured over intra-clutch variation in the war against brood parasites (Stokke et al. 1999). Such polymorphism is the result of subtle variation in multiple aspects of egg colours and patterns, and thus appears to be continuous variation, although it is still polymorphic.

The favouring of this form of polymorphism depends on the means by which host parents detect, recognize, and reject parasitic eggs in their nest. Two recognition mechanisms have been proposed: 1) recognition by learning, in which parents learn the characteristics of their own eggs, probably based on first clutches in life that they lay; 2) recognition by discordance (c.f., concordance or uniformity), in which parents discriminate against the minority eggs in their nests in terms of their different appearance. When the parasitism rate is low, the former mechanism may be effective, because naïve hosts have sufficient opportunity to learn correctly the appearance
of their own eggs. However, when the parasitism rate is high and naïve hosts are likely to be parasitized, if they are not to become egg acceptors they must not learn the characteristics of their own first eggs, because they have a considerable risk of imprinting on cuckoo eggs as their own, even when parasitic eggs look different. Under such circumstances, selection favours hosts that are able to detect parasitic eggs without learning. Uniformity of egg appearance within a clutch should help parents identify and reject parasitic eggs even if the differences are subtle, given that parasitic eggs are a minority within host nests.

In some hosts, between-nest variation is very clear, and thus they exhibit discrete polymorphism. For example, the Ashy-throated Parrotbill Paradoxornis alphonsonianus of East Asia is parasitized by the Common Cuckoo and lays distinctly different blue or white eggs, which differ between laying females. The Common Cuckoo parasitizing the parrotbill, which forms a specific host race, also lays differently coloured eggs to mimic either morph of the host’s eggs (Yang et al. 2010). The frequency of each egg type is predicted to oscillate over time (Takasu 2003; Liang et al. 2012). The Tawny-flanked Prinia Prinia subflava in Central Africa, parasitized by the Cuckoo Finch Anomalospiza imberbis, lays extremely diverse polymorphic eggs. Each female lays eggs that differ dramatically in background colour, spot and line colour, and even in pattern (Spottiswoode & Stevens 2011); thus the morphs differ so much from one another that their eggs appear to be those of different species. These are extreme cases of between-nest egg variation, with within-nest uniformity.

Within-nest egg uniformity plays a central role in the coevolutionary arms races between these hosts and their parasites, particularly in the psychological aspect. Even with polymorphism, accurate mimicry by the parasite should in principle enhance the probability of recognition errors by host parents (Davies et al. 1996; Stevens et al. 2013). However, even if a cuckoo perfectly mimics all of the egg morphs of a host, it would be adaptive for those hosts to have greater between-nest polymorphism because of the stochasticity of mimicry accomplishment. Even if a parasitic female can choose a host nest that contains eggs that her own eggs perfectly mimic (Honzá et al. 2013), she is unlikely to be able to encounter such nests repeatedly during a single breeding season (Liang et al. 2016), and such probability will be reduced when the host produces a greater number of egg morphotypes.

Therefore, once polymorphism has evolved, and hosts have achieved within-nest egg uniformity, the arms race will more greatly favour between-nest egg variation, and thus egg polymorphism should become more diverse over time (Caves et al. 2015). In terms of egg appearance, hosts will defeat parasites in the coevolutionary arms race if they exhibit distinct egg polymorphism as an anti-parasitic defence strategy, as long as the parasites cannot easily target a host’s specific egg morph (Liang et al. 2016). This could advance the coevolutionary arms races to the next stage. In fact, the Cuckoo Finch seems to have acquired a counter-adaptive strategy against egg polymorphism by its host, in which the parasite exploits the recognition rule of uniformity. Some Cuckoo Finch females lay several of their eggs consecutively in the same host’s nest, thereby sometimes outnumbering the host’s eggs (Stevens et al. 2013). In such cases, some of their hosts accept the parasitic eggs even though they fail to accurately mimic their own eggs. These findings jointly indicate that egg uniformity within nests is more important, both for the host to detect parasitic eggs and for the parasite to evade host discrimination, than accurate recognition/mimicry. Interestingly, the Cuckoo Finch also lays polymorphic eggs, but its mimicry appears not to be particularly accurate (Spottiswoode & Stevens 2011). Such dynamism in coevolutionary arms races is also expected at life stages other than eggs (Sato et al. 2015).

Chick polymorphism

Given the advantages of egg polymorphism, polymorphism in chick appearance is also expected to favour hosts when the coevolutionary arms race occurs at the chick stage; this occurs for example in some bronze-cuckoo (genus Chalcites) systems (Langmore et al. 2003; Sato et al. 2010; Tokue & Ueda 2010; Langmore et al. 2011; Sato et al. 2015). The process in which polymorphism is acquired in the coevolutionary arms race at the egg stage may also be applied to that at the chick stage (see Fig. 1A). After a parasite begins to exploit a host, its virulence may trigger the evolution of the host’s discrimination as an anti-parasitic defence (represented by an arrow in Fig. 1A), which leads to the evolution of mimicry in the parasite as a counter-adaptation. As the parasite’s mimicry becomes more accurate, through host discrimination, such accurate mimicry favours polymorphism in the host to avoid the parasite’s mimicry, each morphotype of which may be
A recent finding by Sato et al. (2015) indicates that chick polymorphism plays an important role in the arms race in the Fan-tailed Gerygone *Gerygone flavolateralis* in New Caledonia, which is parasitized by its specialist brood parasite, the Shining Bronze-cuckoo *C. lucidus*. Both host and parasitic chicks have discrete polymorphism in skin coloration: blackish brown and pinkish beige. Since Fan-tailed Gerygone parents discriminate against parasitic chicks, probably by recognizing cuckoo chicks as parasites, such polymorphism would have been acquired in the same manner as that in egg appearance (Fig. 1A).

However, chick polymorphism apparently plays little role (at least presently) in aiding the detection of parasitic chicks by Fan-tailed Gerygone host parents: irrespective of matching skin coloration between parasitic and host chicks, or even under the presence or absence of host chicks, host parents did not fail to eject parasitic chicks from their nests (Sato et al. 2015). Moreover, a portion of host nests contain both types of host chicks, that is, there is within-nest (intra-brood) polymorphism, but parents seem not to misrecognize them as parasites. Considering the key role of within-nest uniformity in rejecting brood parasites, this within-nest polymorphism could lower the fitness of hosts exhibiting polymorphism (Fig. 1B). If skin colour were a cue for host parents to detect parasitic chicks, host chicks of either of the two morphs within a single nest should be recognized as parasites and then ejected from the nest. One possibility is that skin colour polymorphism in chicks is independent of the coevolutionary arms race. However, this scenario seems unfeasible, since skin colour polymorphism is quite rare among birds (Kilner 2006), and in the light of the dynamism of polymorphism in the arms race supported by evidence from the egg stage, which is consistent with evidence found in this system (e.g., chick mimicry and host parental discrimination).

Sato et al. (2015) argued that nestling polymorphism may initially have evolved as a result of the coevolutionary arms race in the same manner as
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polymorphism in the egg stage. However, the expression mechanism of the gene(s) responsible for chick polymorphism, which differs from those for egg polymorphism, would have constrained any advantage of polymorphism in chicks. All of the egg attributes, except the fertilized egg, or the embryo, are maternal traits, thus egg appearance is an extended phenotype of the mother, and there is no genetic variation within a single non-parasitized nest. On the contrary, chick characteristics are in principle determined by inherited paternal and maternal genes and interactions between them. Therefore, as long as the relevant traits are of autosomal inheritance, phenotypes could differ between chicks even if they share exactly the same parents, and thus uniformity within nests could be violated. In the arms race at the chick stage, this heterogeneity between full-siblings would be critically dysfunctional, as it is genetically inevitable, and thus diversifies the consequences of coevolution between egg and chick polymorphism (Fig. 1B). To reject brood parasitism by the Shining Bronze-cuckoo given the presence of within-nest polymorphism, Fan-tailed Gerygone parents need to discriminate against mimetic parasitic chicks finely, while at the same time they need to ignore the distinctly different skin colours of their own progeny. These requirements, caused by chick polymorphism, may have further driven the coevolutionary arms race towards the next step.

Adult polymorphism

Polymorphism is also found among adults in brood parasitic systems. The females of some parasitic cuckoos, such as the Common Cuckoo, exhibit discrete plumage polymorphism (Thorogood & Davies 2012). This polymorphism in the adult parasites can facilitate their egg laying, because host parents that defend their nests would fail, or at least be slow, to recognize the rare morph as a brood parasite. Even if the difference in the latency of host recognition is slight, it should be enough for cuckoo mothers to sneak into host nests and lay their eggs successfully, which could act as negative frequency-dependent selection. Female plumage polymorphism sometimes co-occurs with barred patterning i.e., hawk mimicry (Thorogood & Davies 2013), which may have evolved to deter hosts from attacking (Davies & Welbergen 2008). Therefore, adult brood parasites exploit their hosts’ misperception, combining two kinds of deception in order to protect their eggs.

Egg laying by parasites, without being noticed by host parents, is particularly important for successful parasitism because host parents can damage parasitic eggs in their nests more confidently when noticing the presence of adult parasites around their nests (Moksnes et al. 1990). Thus, this should also be an important stage in the coevolutionary arms race between brood parasites and their hosts. Defending their nests from brood parasites is the very frontline for hosts as an anti-parasitic defence strategy. Of course such defence incurs vigilance costs, because host females need to spend time on foraging in order to produce their eggs, and because remaining close to the nest could lure predators or even brood parasites to the nest. Hosts may have become well adapted to such constraints, as they are able to alter their level of alertness in a flexible manner in response to the density of brood parasites through social transmission of information (Brooke et al. 1998; Davies & Welbergen 2009). This adaptation has lead to the deception by adult cuckoos, and could be one of substantial drivers of the coevolutionary arms race. In fact, it has been revealed recently that female Cuckoo Finches resemble non-parasitic finches in appearance; this resemblance functions as a form of aggressive mimicry to facilitate parasitic egg laying (Feeney et al. 2015). In conclusion, polymorphism in brood parasites indicates the existence of a substantial selective force, which is imposed by recognition of brood parasites by their hosts.

Beyond Behavioural Ecology

Finally, I emphasize the need to combine the known facts, revealed mainly by behavioural ecological studies, with approaches devised to reveal proximate causes, by means of genetics and genomics, or cognitive mechanisms.

Genetics

In order to further our understanding of the coevolutionary arms race between avian brood parasites and their hosts, I propose synthesising three levels of evolutionary research in brood parasitism studies: these are 1) phenotype and behaviour; 2) theory and dynamics; 3) genomes and mechanisms. Most brood parasitism studies have focussed mainly on levels 1 and 2, namely, ultimate causes, but few studies have unveiled genetics, except for those related to phylogeny and lineages (Gibbs et al. 2000; Sorenson & Payne 2002; Sorenson et al. 2003; Fossey et al. 2011, 2016), or pedigree and population genetics (Gosler et al. 2000; Sato et al. 2015). However, recent advances
in biology require researchers to present more substantial evidence, such as genomes or physiological processes, i.e., proximate causes, along with ultimate causes.

Under these circumstances, we do not need to be pessimistic because advances in biology also help us target candidate processes. On the one hand, for example, the genetic bases of skin and hair colour have been extensively studied among mammals, and thus there are some well-known genes. Brown and black are usually produced by melanosomes composed of eumelanin, whose expression is controlled by a melanocortin receptor on the cell (melanocyte) membrane. Variation in the gene responsible for the melanocortin receptor, called \(MC1R\), causes variation, i.e., polymorphism, in skin or hair coloration, which is also applicable to avian plumage coloration (San-Jose et al. 2015). Yellow or red are caused by pheomelanin, controlled by a gene called \(Agouti\) (\(ASIP\)) (Lu et al. 1994), which is also known to express itself in avian feather colour production (Oribe et al. 2012). On the other hand, egg colours and patterns are produced in a completely different process from that for feather and skin. Eggs are coloured in the oviduct of mother birds with bile-derived pigments, such as biliverdine (Kilner 2006). The process is more complicated than that for feather and skin, but such knowledge of proximate causes should help determine the candidate genes.

To summarize, to draw the whole picture of the coevolutionary arms race between avian brood parasites and their hosts, we must go beyond ecology, and thankfully, with the help of advances in biology, this is the right time.

Psychology

There is one further aspect to explore – the psychological aspect of the coevolutionary arms race. Although this topic has long been the main issue in brood parasitism studies (Rothstein 1974; Lotem 1993; Davies et al. 1996; Stokke et al. 1999; Lahti & Lahti 2002; Tanaka et al. 2005; Moskát et al. 2010), by incorporating polymorphism, substantial progress could be made. For example, based on experimental and psychophysical (Tanaka 2015) approaches, Spottiswoode and Stevens (2011) revealed that egg polymorphism affects the evolution of the cognitive ability of host parents. The authors found that a host of the Cuckoo Finch without egg polymorphism had finer discrimination ability against alien eggs than another host with egg polymorphism. This study suggests that the cognitive ability of host parents is the main issue of the coevolutionary arms race, but it might be difficult to reveal such a parental tendency without discrete polymorphism (i.e., if only with continuous variation of egg appearance).

Conclusion

Studying polymorphism can facilitate synthesis with proximate approaches, such as genomics and psychology, and thus may allow researchers to grasp the entire picture of the arms race. Finally, by focusing on polymorphism, we can approach the dynamics of the coevolutionary arms race between avian brood parasites and their hosts more closely than ever in every biological aspect.

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