



# DIGITAL ACCESS TO SCHOLARSHIP AT HARVARD

## Response to Langmore and Spottiswoode: "Visual Trickery in Avian Brood Parasites"

The Harvard community has made this article openly available.  
[Please share](#) how this access benefits you. Your story matters.

|                          |  |
|--------------------------|--|
| <b>Citation</b>          | Edwards, Scott V. 2012. "Response to Langmore and Spottiswoode: 'Visual Trickery in Avian Brood Parasites'" (Afterword, Chapter 6). In <i>Host Manipulation by Parasites</i> , ed. David P. Hughes, Jacques Brodeur, and Frédéric Thomas, 116-118. New York: Oxford University Press.  |
| <b>Published Version</b> | <a href="http://ukcatalogue.oup.com/product/9780199642236.do#.UEzqTxjdDOE">http://ukcatalogue.oup.com/product/9780199642236.do#.UEzqTxjdDOE</a>  |
| <b>Accessed</b>          | February 19, 2015 1:56:56 PM EST   |
| <b>Citable Link</b>      | <a href="http://nrs.harvard.edu/urn-3:HUL.InstRepos:11870357">http://nrs.harvard.edu/urn-3:HUL.InstRepos:11870357</a>  |
| <b>Terms of Use</b>      | This article was downloaded from Harvard University's DASH repository, and is made available under the terms and conditions applicable to Other Posted Material, as set forth at <a href="http://nrs.harvard.edu/urn-3:HUL.InstRepos:dash.current.terms-of-use#LAA">http://nrs.harvard.edu/urn-3:HUL.InstRepos:dash.current.terms-of-use#LAA</a> |

*(Article begins on next page)*

## **Response to Langmore and Spottiswoode: “Visual trickery in avian brood parasites”**

By Scott V. Edwards

Alternative title: **Genetics and the evolutionary history of avian brood parasitism**

The tricks that parasites play on their hosts to gain access to reproductive opportunities are among the most elaborate and sinister in the world of behavior. As an evolutionary biologist, I find that instances of visual mimicry – of insects or frogs mimicking leaves, for example – often stretch my credulity in the power of natural selection to hone and refine the mimicry to the smallest of details. I wonder how it could be that mimicry in nature is often so perfect – was the advantage of a slightly better mimic really so great as to render an imperfect mimic less fit? As a population geneticist, I like to imagine that genetic drift – an ever present force in all but the largest populations, and most likely a permanent fixture of the genetics of all vertebrates (along other forces such as linkage of genes to one another on chromosomes), must place constraints on the efficacy of natural selection to increase the match between mimic and host. After all, population genetics and behavior can sometimes be uneasy bedfellows – the one frequently eschewing simple deterministic scenarios involving linear paths to adaptation unfettered by genetic constraints, and the other reveling in them. As an ornithologist, however, the often unbelievable yet sometimes contradictory and surprising outcomes of host-parasite arms races come into better focus. Birds are, after all, excellent model

systems for the study and experimental manipulation of behavior in general and nest parasitism in particular. Langmore and Spottiswoode's chapter on visual manipulation of hosts by avian brood parasites nicely illustrates the amazing diversity of tricks used by parasites to gain access to nests and parental behaviors of their hosts, the varied responses of avian hosts to these parasites, yet how much we still don't understand about these intricate interactions. In particular, I argue, we need to understand the genetics of avian brood parasite adaptations, and their realization over broad phylogenetic, temporal and geographic landscapes, in order to better understand the dynamics and contingencies underlying these remarkable adaptations.

The chapter opens with a good example of how avian parasites utilize different strategies to achieve access to host nests. (Actually, I very much dislike the anthropomorphic term 'strategy' in biology but I will here and elsewhere let my guard down). Despite the fact that most brood parasites try to mimic "harmless or inviting" species so as to gain access to nests (p. xx), Langmore and Spottiswoode point out that avian parasites such as cuckoos frequently possess the plumage, morphology and flight behavior of predatory species such as hawks and falcons, an hypothesis from natural history observation that now has experimental support (Welbergen and Davies 2011). One wonders why the incidence of Batesian mimicry – when a (physically) harmless species mimics one that could cause harm – is so high in the cuckoos. It is intriguing that the clade of cuckoos – non-passerine birds with medium to large body sizes compared to many passerines – have sometimes converged on predatory birds with similar body sizes. Perhaps the morphological

distance that needs to be traversed by cuckoos in order to mimic hawks is less than in other clades? Or are there a suite of mutations deep in the cuckoo clade that makes such visual mimicry easier to achieve, even convergently across multiple lineages?

As Langmore and Spottiswoode point out, cuckoos are among the best studied avian brood parasites, providing excellent examples of egg mimicry and within-species egg diversification, and recently providing the first well-studied example of host mimicry at the chick stage (Langmore et al. 2003; reviewed in Langmore and Kilner 2010). For example, in the classical scenario for many cuckoo species, selection for egg mimicry by parasites is driven by a history of host-rejection of conspicuous or outstanding eggs in the clutch. But some host species, such as Superb Fairy Wren (*Malurus cyaneus*) appear to be unable to identify and reject conspicuous eggs when placed in the nest experimentally. Such observations may mean that egg mimicry by Horsfield's Bronze-Cuckoos (*Chalcites basalis*), a common parasite of Fairy Wrens, is driven not by host selection but by evasion of additional cuckoo parasites, which often remove an egg from a clutch before depositing their own. As Langmore and Spottiswoode show, the multiple and often unexpected hypotheses on the origins of egg mimicry constitute a sort of two-sided mirror through which nearly every adaptation of brood parasites and their hosts can be viewed.

A useful perspective on the speed and mechanisms by which egg mimicry arises in brood parasites comes from molecular methods. Several species of cuckoo

exhibit host races, or 'gentes', differentiated forms that lay distinct egg types that closely match eggs of their hosts. Such forms are hypothesized to be differentiated at genes underlying egg color and possibly other traits associated with parasitism. Indeed, such gentes have been shown to exhibit mild genetic differentiation in maternally inherited mtDNA in some populations of cuckoos and in indigobirds, the latter among closely related parasitic species (reviewed in Sorenson and Payne 2002). Still, the extent of differentiation in mtDNA is not large and does not approach the pattern of fixed genetic differences that the egg colors themselves imply. Phylogeographic patterns such as these suggest that the evolution of cuckoo gentes has proceeded rapidly and that no stable associations between parasite and host exist in some species, including Horsfield's Bronze-Cuckoo (Joseph et al. 2002). This conclusion in turn suggests that the intricate host-parasite interactions and multiple rounds of co-evolution hypothesized by Langmore and Spottiswoode to occur in many avian brood parasite systems have arisen very rapidly and recently, and may not persist for long periods before being obliterated by environmentally contingent demographic or geographic shifts in host or parasite. Given this potentially short time frame, one wonders whether learning or some type of cultural evolution could facilitate the rapid spread of parasite-rejection by some hosts. Reviewing the evidence and models, Langmore and Spottiswoode suggest that a role for learning in the evolution of parasite rejection is likely small and would work only under a restricted set of evolutionary parameters, including low host chick survival. Still, the precise fitness loss experienced by hosts under parasitism can be a complex

function of many demographic parameters (Servedio and Hauber 2006), and further studies on the role of learning in host rejection are clearly needed.

With its strictly maternal inheritance in birds and other vertebrates, mtDNA is a useful proxy for the genes underlying egg color, especially if the avian W chromosome, with which mtDNA is effectively linked in birds, is involved. Still, with its lack of frequent recombination for much of its length in birds, the W chromosome may not be the whole story behind variation in egg coloration of brood parasites and genetic interactions with autosomal loci have been hypothesized (Sorenson and Payne 2002). Recently, a polymorphic population of cuckoo genes was shown to exhibit mild but significant differentiation at autosomal microsatellites (Fossoy et al. 2011). Given the bias toward low estimates of differentiation (such as  $F_{st}$ ) for highly polymorphic microsatellites as compared to sequence-based markers (Charlesworth 1998; Brito and Edwards 2009), detecting such differentiation among such closely related populations is indeed a feat, and bodes well for future genomic studies aimed at finding the genes underlying egg shell coloration and other adaptations of avian brood parasites (Yuan and Lu 2007).

And to be sure, the mapping, sequencing and evolutionary study of these still hypothetical brood parasite and host response genes is of great relevance to the study of avian brood parasitism. As with any behavioral or morphological adaptation, understanding the genetic basis can clarify a lot about how and when the adaptation arose in a particular lineage, how it co-evolves with other traits and how it is maintained and potentially lost over time: think of the marvelous work on

the genetics of social behavior in *Dictostylium* (Sucgang et al. 2011). I never did adhere to a strict interpretation of Paul Sherman's (1988) famous four-fold distillation of the sources of adaptations, involving evolutionary origins, ontogenetic processes, mechanisms and functional consequences, because I view these four levels as so inextricably linked – potentially genetically - as to make their clean separation nearly impossible, particularly when one tries to quantify these aspects of adaptation. This is why understanding the genomics of brood parasitism will be helpful for interpreting host and parasite behavior, however distant that goal is. By elucidating the genetic mechanisms underpinning the many brood parasitic adaptations and host responses discussed by Langmore and Spottiswoode, they will help us make sense of – indeed, quantify - their evolutionary history, constraints and contingencies, thereby making all the more realistic our evolutionary scenarios of these wildly diverse traits.

## References

- Brito, P., and S. V. Edwards. 2009. Multilocus phylogeography and phylogenetics using sequence-based markers. *Genetica* 135:439-455.
- Charlesworth, B. 1998. Measures of divergence between populations and the effect of forces that reduce variability. *Molecular Biology and Evolution* 15:538-543.
- Fossoy, F., A. Antonov, A. Moksnes, E. Roskaft, J. R. Vikan, A. P. Moller, J. A. Shykoff et al. 2011. Genetic differentiation among sympatric cuckoo host races: males matter. *Proceedings of the Royal Society B-Biological Sciences* 278:1639-1645.
- Joseph, L., T. Wilke, and D. Alpers. 2002. Reconciling genetic expectations from host specificity with historical population dynamics in an avian brood parasite, Horsfield's Bronze-Cuckoo *Chalcites basalis* of Australia. *Molecular Ecology* 11:829-837.
- Langmore, N. E., S. Hunt, and R. M. Kilner. 2003. Escalation of a coevolutionary arms race through host rejection of brood parasitic young. *Nature* 422:157-160.

- Langmore, N. E., and R. M. Kilner. 2010. The coevolutionary arms race between Horsfield's Bronze-Cuckoos and Superb Fairy-wrens. *Emu* 110:32-38.
- Servedio, M. R., and M. E. Hauber. 2006. To eject or to abandon? Life history traits of hosts and parasites interact to influence the fitness payoffs of alternative anti-parasite strategies. *Journal of Evolutionary Biology* 19:1585-1594.
- Sherman, P. W. 1988. The levels of analysis. *Animal Behaviour* 36:616-619.
- Sorenson, M. D., and R. B. Payne. 2002. Molecular genetic perspectives on avian brood parasitism. *Integrative and Comparative Biology* 42:388-400.
- Sucgang, R., A. Kuo, X. J. Tian, W. Salerno, A. Parikh, C. L. Feasley, E. Dalin et al. 2011. Comparative genomics of the social amoebae *Dictyostelium discoideum* and *Dictyostelium purpureum*. *Genome Biology* 12: R20.
- Welbergen, J. A., and N. B. Davies. 2011. A parasite in wolf's clothing: hawk mimicry reduces mobbing of cuckoos by hosts. *Behavioral Ecology* 22:574-579.
- Yuan, Q.-Y., and L.-Z. Lu. 2007. Progresses in inheritance of genes for avian eggshell color. *Yichuan* 29:265-268.