

# Visual trickery in avian brood parasites

Naomi E. Langmore and Claire N. Spottiswoode

---

## 6.1 Introduction

Visual mimicry is a strategy deployed by a wide range of taxa, from spiders that mimic the ants they hunt (Nelson and Jackson 2006), to cross-dressing males in bluegill sunfish (Dominey 1980), and harmless snakes that mimic the vibrant colors of venomous snakes (Harper and Pfenning 2008) (see Chapter 11). Although visual mimicry is widespread amongst invertebrates, and to a lesser extent fish, amphibians, and reptiles (Ruxton et al. 2004), it is generally a rare phenomenon among birds (but see e.g., Dumbacher and Fleischer 2001). However, the avian brood parasites provide a notable exception. Several recent field studies, combined with new techniques for quantifying mimicry and modeling the visual perception of hosts, demonstrate that brood parasites have evolved hitherto unknown forms of visual mimicry as means of manipulating their hosts at every stage of host-parasite interactions.

Avian brood parasites lay their eggs in the nests of other birds, and thereafter abandon their young to the care of the host. The costs of parasitism to the host may be (1) negligible, when incubation of an additional egg is the only care required (Lyon and Eadie 2004); (2) moderate, when the parasitic chick is reared alongside the host young (non-evicting parasites); and (3) severe, when the parasitic chick kills or evicts all the host young from the nest (evicting parasites). In general, with increasing costs of parasitism, host defenses become more sophisticated, in turn selecting for ever more elaborate trickery on the part of the parasite to fool the host

into rearing its young. Thus we generally see the most advanced parasite recognition systems amongst hosts of evicting parasites, which in turn select for highly accurate visual mimicry by parasites to evade host detection.

However, host defenses are not the only selective agent responsible for the evolution of visual mimicry in brood parasites. Mimicry can also arise to facilitate exploitation of parent-offspring channels of communication, ensuring that the parasite chick is able to elicit adequate care from its foster parents (parasite “tuning,” Davies 2011). Mimicry for this purpose is equally likely to arise in evicting and non-evicting parasites, and was termed sequential evolution mimicry by Grim (2005), to distinguish it from mimicry that arises through a coevolutionary arms race. However a recent hypothesis suggests that this form of mimicry could also ultimately lead to a coevolutionary arms race between parasites and hosts (see Hauber and Kilner 2007, Section 6.5 below).

Here, we will first consider how visual mimicry evolves as an outcome of a coevolutionary arms race between parasites and their hosts, driven by host defenses against parasitism. We will describe how host defenses have selected for mimicry by brood parasites in all three successive stages of the parasitism process; gaining access to host nests (Section 6.2), the egg stage (Section 6.3), and the chick stage (Section 6.4). Second, we will discuss how visual mimicry can evolve to facilitate exploitation of channels of communication between host parents and offspring (Section 6.5). Finally, in Section 6.6 we will consider the different challenges faced by generalist versus specialist parasites, and the strategies used

by generalists to solve the problem of how to mimic a diversity of morphologically distinct hosts.

## 6.2 Accessing host nests

The process of laying an egg is fraught with challenges for a parasitic bird. Hosts typically mob parasites violently, and this can provide an effective defense against parasitism (Welbergen and Davies 2009), as well as causing injury (Davies and Brooke 1988b; Welbergen and Davies 2008; Wyllie 1981) or even death (Molnar 1944, Moyer 1980) to the parasite. However, a recent study demonstrated that cuckoos have evolved a clever visual trick to inhibit host aggression, thereby facilitating access to host nests.

Naturalists have long been aware that several cuckoo species bear a striking resemblance to sympatric aggressive or predatory birds (e.g., the drongo cuckoo *Surniculus lugubris* and the drongo *Dicrurus macrocercus*, the large hawk-cuckoo *Cuculus sparverioides* and the besra sparrowhawk *Accipiter virgatus*, the common hawk-cuckoo and the shikra *Accipiter badius*, the common cuckoo *Cuculus canorus* and the Eurasian sparrowhawk *Accipiter nisus*, Fig. 6.1; Johnsgard 1997).

The similarities encompass size, shape, plumage color and pattern, and even flight behavior (Davies and Welbergen 2008). Several hypotheses have been proposed to explain this resemblance, including convergent evolution, inducement of mobbing to facilitate location of potential hosts, protection against hawk attacks, and inhibition of mobbing by hosts (Craib 1994; Davies and Welbergen 2008; Wallace

1889; Wyllie 1981). Resemblance to predatory birds is more common in parasitic than non-parasitic cuckoos, and evolved after the evolution of brood parasitism (Krüger et al. 2007; Payne 1967), favoring hypotheses that suggest this form of mimicry plays some role in brood parasitism. Recently, an experimental test of the functional significance of hawk mimicry by cuckoos was undertaken for the first time (Welbergen and Davies 2011). Plumage manipulations of taxidermic models revealed that the hawk-like barring on the breasts of common cuckoos inhibits approach by their reed warbler *Acrocephalus scirpaceus* hosts, thus reducing harassment of cuckoos during nest parasitism. When the barred underparts were concealed, reed warblers approached the model cuckoo more closely and mobbed it more intensely. This indicates that hawk-like barring is adaptive in the context of brood parasitism and provides rare experimental evidence of Batesian mimicry in birds.

## 6.3 The egg stage

The egg stage in the battle between brood parasites and hosts provides some of the most compelling and widely-known examples of visual trickery in nature: a cuckoo egg superbly blending into the clutch of its unsuspecting host is a typical and defining image. Parasitic mimicry of host eggs has arisen independently in six of the seven groups in which interspecific brood parasitism has evolved independently in birds. The seventh is the black-headed duck *Heteronetta atricapilla* of South America, a



**Figure 6.1** Many cuckoo species show a physical resemblance to predatory or aggressive birds. Here, the common cuckoo (center, photo: Roy and Marie Battell) bears a superficial resemblance to the peregrine falcon *Falco peregrinus* (left, photo: Jack Wolf) and the Eurasian sparrowhawk *Accipiter nisus* (right, photo: Steve Grimwade).

fascinating exception (Lyon and Eadie 2004) which we consider in more detail below.

The common cuckoo and its hosts provide predictably the longest history of thought on the evolution of visual mimicry in parasitic eggs. The remarkable resemblance between cuckoo eggs of different “strains” (or “gentes,” singular “gens”; Newton 1896) and the eggs of their corresponding host species was first commented upon during the eighteenth century, but many early observers attributed it to common elements of diet between host and parasite, rather than any deceptive function (reviewed by Schulze-Hagen et al. 2009). A series of authors, many of them egg collectors, began to speculate about how host–parasite resemblance could serve to reduce egg rejection by hosts (Schulze-Hagen et al. 2009). Systematic egg rejection experiments were pioneered in brown-headed cowbird *Molothrus ater* hosts (e.g., Rothstein 1975; Rothstein 1982), and such an experimental approach applied to common cuckoo hosts elegantly showed that color and pattern mimicry in common cuckoo eggs is under selection from discriminating hosts: host species in which the cuckoo lays a more closely mimetic egg also showed stronger discrimination against foreign eggs (Brooke and Davies 1988; Davies and Brooke 1989a). This provided compelling evidence that egg mimicry is a host-specific adaptation that has arisen through coevolutionary interactions between parasitic exploitation and host counter-defense, and has led to the diversification of cuckoo host-specific gentes.

Subsequent to these classic experimental studies, understanding of avian vision and visual perception has much improved (e.g., Endler and Mielke 2005; Vorobyev and Osorio 1998). The advance of spectrophotometry and visual modeling techniques over the last decade has helped to reveal examples of subtlety in visual trickery by brood parasites that could not have been anticipated by the human eye alone. Early application of spectrophotometry to quantify eggshell reflectance, for example, suggested potential mimicry between red-chested cuckoo *Cuculus solitarius* and host eggs that appear dissimilar to the human eye (Cherry and Bennett 2001), and revealed previously undetected host-specific adaptation to multiple host species in pallid

cuckoos *Cuculus pallidus* (Starling et al. 2006). Spectrophotometry improves on human visual assessment since it is objective and incorporates ultra-violet wavelengths invisible to humans, but does not consider how a signal is processed by a bird’s visual system, and hence provides imperfect insight into mimicry from a bird’s perspective. Perceptual models of avian vision improve on spectrophotometry alone by processing spectrophotometric data in the light of current understanding of avian color vision, to generate estimates of color differences as they should be perceived by a bird. The last few years have seen a flowering of the application of such models to studies of brood parasitic mimicry in various systems (e.g., Cassey et al. 2008; Avilés 2008; Spottiswoode and Stevens 2010; Langmore et al. 2009; Langmore et al. 2011), and some of their findings will appear later in this chapter.

Avian perceptual modeling has also allowed classic experimental work, which relied on scoring mimicry using human observers, to be revisited in the light of improved understanding of avian vision. The original conclusion has remained unaltered: host species previously shown to have the strongest levels of egg rejection are parasitized by cuckoos laying eggs that are a more mimetic to a bird’s eye, too, and this has held true both for egg patterning (Stoddard and Stevens, 2010) and egg color (Stoddard and Stevens, 2011). However, perceptual modeling has provided additional insights that could not have been detected using human assessment alone: for example, the egg color distribution of host species and their corresponding cuckoo gens overlap most in avian perceptual color space in host species that show the strongest rejection behavior (Stoddard and Stevens, 2011). Moreover, as color mimicry improves, so does pattern mimicry, perhaps implying that hosts rely increasingly on pattern cues when mimicry is refined to the point that colors become nearly indistinguishable to a bird’s eye (Stoddard and Stevens, 2011).

Host discrimination against foreign eggs based on visual traits has now been demonstrated experimentally using similar approaches in a wide variety of interspecific brood parasitic systems (listed in Table 6.1). Egg rejection experiments are necessary

**Table 6.1** Parasitic systems in which egg rejection by hosts has been experimentally investigated, and whether or not parasitic eggs show host mimicry. "Specialist" is used to refer to parasites that specialize either on a single host or a group of very closely-related hosts in the same genus (e.g., *Acanthiza* for shining bronze-cuckoo and *Laniarius* for black cuckoo). "Gentes" here is used to refer to host-specific variation in phenotype, in most cases without any data on whether genetically defined strains of females exist. "Polymorphism" here is used to refer to extreme inter-individual variation in phenotype, following Kilner (2006), rather than classic discrete polymorphisms established to have a simple genetic basis. "Visual" cues here refer to color and patterning, rather than egg size or shape.

Species	Specialist or generalist parasite	Parasite shows gentes	Parasite eggs resemble host's	Host eggs polymorphic	Host egg rejection based on visual cues
<b>Ducks (Anatidae)</b>					
Black-headed duck <i>Heteronetta atricapilla</i>	Generalist	No	No	No	Yes <sup>1</sup>
<b>Old World cuckoos (Cuculidae:</b>					
<b>Cuculinae: Cuculini)</b>					
Horsfield's bronze-cuckoo <i>Chalcites basalis</i>	Generalist	No	Yes	No	No <sup>2, 3</sup>
Shining bronze-cuckoo <i>Chalcites lucidus</i>	Specialist	No	No	No	No <sup>2, 4</sup>
Diederik cuckoo <i>Chrysococcyx caprius</i>	Generalist	Yes	Yes	Sometimes	Yes <sup>5-8</sup>
Klaas's cuckoo <i>Chrysococcyx klaas</i>	Generalist	Yes	Yes	Sometimes	Yes <sup>8</sup>
Common cuckoo <i>Cuculus canorus</i>	Generalist	Yes	Sometimes	Sometimes	Sometimes <sup>9-11</sup>
Black cuckoo <i>Cuculus clamosus</i>	Specialist	Maybe	Yes	Sometimes	Yes <sup>8</sup>
African cuckoo <i>Cuculus gularis</i>	Specialist	No	Yes	Yes	Yes <sup>8, 12</sup>
Oriental cuckoo <i>Cuculus optatus</i>	Generalist	Yes	Sometimes	No?	Yes <sup>13</sup>
Pallid cuckoo <i>Cuculus pallidus</i>	Generalist	Yes	Yes	Yes	Yes <sup>14</sup>
Asian lesser cuckoo <i>Cuculus poliocephalus</i>	Generalist	Yes	Sometimes	No?	Yes <sup>13</sup>
Red-chested cuckoo <i>Cuculus solitarius</i>	Generalist	Yes	Sometimes	Sometimes	Sometimes <sup>15</sup>
Common koel <i>Eudynamys scolopaceus</i>	Specialist	No	Yes	No	Yes <sup>16</sup>
<b>Old World cuckoos (Cuculidae: Cuculinae:</b>					
<b>Phaenicophaeini)</b>					
Great spotted cuckoo <i>Clamator glandarius</i>	Generalist	No	Sometimes	Sometimes	Yes <sup>8, 17, 18</sup>
Jacobin cuckoo <i>Clamator jacobinus</i>	Generalist	No (in Africa)	No	No	No <sup>8, 19</sup>

### Cowbirds (Icteridae)

Bronzed cowbird <i>Molothrus aeneus</i>	Generalist	No	No	No?	Sometimes <sup>20</sup>
Brown-headed cowbird <i>Molothrus ater</i>	Generalist	No	No	No	Sometimes <sup>21, 22</sup>
Shiny cowbird <i>Molothrus bonariensis</i>	Generalist	No	No	No	Sometimes <sup>23, 24</sup>
Giant cowbird <i>Molothrus oryzivorus</i>	Generalist	No	Yes	Yes	Yes <sup>25</sup>
Screaming cowbird <i>Molothrus rufoaxillaris</i>	Specialist	No	Yes	Yes	No <sup>26</sup>

### Parasitic Finches (Viduidae)

Cuckoo finch <i>Anomalospiza imberbis</i>	Generalist	Yes	Yes	Yes	Yes <sup>27</sup>
---	------------	-----	-----	-----	-------------------

---

### References

- <sup>1</sup> Lyon and Eadie (2004). <sup>2</sup> Brooker and Brooker (1989). <sup>3</sup> Langmore et. al. (2003). <sup>4</sup> Langmore et al. (2005). <sup>5</sup> Victoria (1972). <sup>6</sup> Lahti and Lahti (2002). <sup>7</sup> Jackson (1998). <sup>8</sup> Noble (1995).  
<sup>9</sup> Brooke and Davies (1988). <sup>10</sup> Yang et al. (2010). <sup>11</sup> Moksnes et al. (1990). <sup>12</sup> Tarboton (1986). <sup>13</sup> Higuchi (1989). <sup>14</sup> Landstrom et al. (2010). <sup>15</sup> Honza et al. (2005).  
<sup>16</sup> Sumit Sinha and Suhel Quader. Unpublished Data. <sup>17</sup> Soler and Møller (1990). <sup>18</sup> Alvarez et al. (1976). <sup>19</sup> Krüger (2011). <sup>20</sup> Peer et al. (2002). <sup>21</sup> Rothstein (1975). <sup>22</sup> Rothstein (1982).  
<sup>23</sup> Mermoz (1994) <sup>24</sup> Fraga (1985). <sup>25</sup> Cunningham and Lewis (2005). <sup>26</sup> Fraga (1998). I <sup>27</sup> Spottiswoode and Stevens (2010).

because similarity between host and parasite eggs may arise through mechanisms other than selection (reviewed by Grim 2005), and because selection for mimicry can come from other quarters than host rejection. Table 6.1 shows that there is abundant evidence that egg discrimination is a widespread defense in host species, and has repeatedly selected for parasitic mimicry. To date, the only interspecific parasitic group in which visual mimicry appears to exist (at least in one species), but no experimental investigations have yet been carried out, is the honeyguides (Indicatoridae): the green-backed honeybird *Prodotiscus zambeziæ* lays blue or white eggs, as does its white-eye (*Zosterops* spp.) hosts (Vernon 1987). Selection for host-specific mimicry may result in very different evolutionary outcomes for the parasite: while in many brood parasites (including numerous cuckoo species), multiple conspecific strains or "gentes" of host-specialists are maintained within the same species, in other systems host-specific mimicry may have resulted in parasitic speciation; we will return to these alternatives later in Section 6.6.

Could visual trickery at the egg stage have evolved in response to pressures other than host defenses? At least two other possible agents of selection for mimicry have been proposed. The first is cuckoos themselves (Davies and Brooke 1988). This could arise through multiple parasitism, where more than one parasitic individual attempts to lay in the same host nest. When the second-laid parasite would suffer from the presence of the first (either through nestling death, or competition), selection should favor the female parasite herself to selectively destroy mismatched eggs, thus ensuring a clear path for her own offspring. Although there have been several experimental tests of this idea in cuckoos, none have found support for the hypothesis (Davies and Brooke 1988; Davies 1999; Langmore and Kilner 2009). This hypothesis might be more applicable under conditions where multiple parasitism is common, as well as (as is the case in cuckoos) the costs of multiple parasitism to the second-laying female being high.

The second alternative hypothesis is that nest predators may impose selection for mimicry via crypsis, if mismatches in appearance within a clutch

render it more conspicuous (Wallace 1889). While there is some evidence that nest predators sometimes select for egg crypsis in entire clutches of non-parasitic species (reviewed by Kilner 2006), this idea as applied to within-clutch disparity has received no support to date, as several studies have failed to find any effect of mismatched experimental eggs on nest predation rates (Swynnerton 1918; Davies and Brooke 1988; Mason and Rothstein 1987; Davies 1992), nor any interspecific evidence that species with higher levels of natural intra-clutch variability suffer higher predation (Avilés et al. 2006b). Experimental tests of this idea are admittedly difficult in rejecting hosts, because mismatched eggs can be rejected too quickly to allow predators a chance to strike (Davies and Brooke 1988); this underscores the importance of host rejection as a selection pressure many (but clearly not all) parasitic species face during *every* breeding attempt.

Thus the weight of evidence suggests that egg mimicry typically arises from a coevolutionary cycle in which hosts gain a fitness advantage from rejecting mismatched eggs, resulting in selection for parasitic mimicry, which in turn results in selection on hosts to evolve ever more finely-tuned egg discrimination. Egg rejection at the incubation stage, however, is a function not only of the absolute discrimination ability of the host. It is also a function of the degree of visual discrepancy between parasitic and host eggs, which hosts have the potential to manipulate in counter-defense against a mimetic parasite. This idea was first put forward by one of the pioneers of egg rejection experiments, Charles Swynnerton, who while farming in eastern Zimbabwe nearly a century ago wrote with great clarity,

"I doubt whether [mimicry] would always end the matter, for, when a Cuckoo's egg became indistinguishable from its host's, variation in the latter would still afford the means of distinguishing it from the Cuckoo's, and it is even imaginable that a race may in some cases have taken place between the host's eggs and those of the overtaking Cuckoo." (Swynnerton 1918).

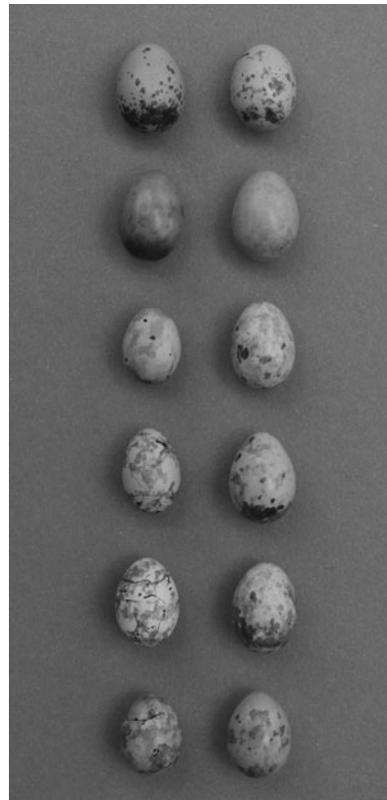
Thus, selection should not only favor more discriminating hosts, but also hosts that lay eggs that

differ in appearance from parasitic eggs, favoring an increase in inter-clutch variability. Additionally, egg discrimination might be facilitated by reduced variation within individuals: selection from brood parasites should favor a decrease in within-clutch phenotypic variability such that parasites are easier to spot, and to avoid mistakenly rejecting a non-parasitic egg (Davies and Brooke 1989b).

These paired predictions have received several tests in the hosts of the common cuckoo, at the level of species, populations, and individual clutches. At the interspecific and population level there is broad agreement that a history of parasitism by the common cuckoo is associated with subtly higher inter-clutch and, less consistently, lower intra-clutch variability (e.g., Soler and Møller 1996; Øien et al. 1995; Stokke et al. 2002). Within species, a fully experimental study has clearly supported the hypothesis that a decrease in within-clutch variability is associated with improved ability to detect foreign eggs (Moskát et al. 2008), although the numerous correlational studies to date have provided very mixed support (Cherry et al. 2007a; Kilner 2006; Landstrom et al. 2010). It has even been proposed that *increased* within-clutch variability might improve detection of parasitic eggs by allowing hosts to label each of their own eggs with an individual, egg-specific rather than clutch-specific “signature” (Cherry et al. 2007a).

However, hosts of the common cuckoo in Europe all lay relatively invariable eggs compared to some other parasitic systems. By contrast, one common cuckoo host in China, the ashy-throated parrotbill *Paradoxornis alphonsianus*, appears to have evolved discrete polymorphisms in egg appearance, laying immaculate white, blue, or pale blue eggs (Yang et al. 2010). In other parasitic systems, diversity in egg appearance is greater still, involving both color and pattern, and not necessarily forming discrete polymorphisms: these include *Ploceus* weavers parasitized by diederik cuckoos *Chrysococcyx caprius* (Victoria 1972), fork-tailed drongos *Dicrurus adsimilis* parasitized by African cuckoos *Cuculus gularis* (Tarboton 1986, C.N.S. unpubl. data), and *Prinia* and *Cisticola* warblers parasitized by cuckoo finches *Anomalospiza imberbis* (Spottiswoode and Stevens 2010); in the last-mentioned, analyses of egg colors

using visual modeling showed that egg color variation is also continuous when perceived by a bird, rather than falling into distinct morphs (Fig. 6.2). In one host of the diederik cuckoo, the village weaver *Ploceus cucullatus*, there is especially clear evidence that variability in egg appearance has responded to selection from brood parasites: introduced populations released from parasitism pressure show both an increase in within-clutch variability and a decrease in between-clutch variability relative to their ancestral, parasitized populations (Lahti 2005), which compromises the weavers’ ability to reject foreign eggs (Lahti 2006). We might speculate that the remarkable phenotypic diversity in the above-mentioned systems is an escalated host defense



**Figure 6.2** Eggs of parasitic cuckoo finches (right column) and two host species (left column). The top two rows are from red-faced cisticola nests and the bottom four rows from tawny-flanked prinia nests; note the extensive variation both between and within host species, mimicked by the parasite (photo: Claire Spottiswoode). See also Plate 10.

reflecting a probably much more ancient origin of brood parasitism in the tropics (and in Africa in particular) compared to Europe (Rothstein 1992).

In all the systems mentioned above, the parasite itself is able to reproduce a broad range of host phenotypes; for example, common cuckoos parasitizing ash-throated parrotbills lay immaculate white or blue eggs (Yang et al. 2010), and cuckoo finches parasitizing tawny-flanked prinias *Prinia subflava* lay eggs with red, blue, or white backgrounds, broadly mimicking those of the prinia but with cruder egg markings that lack the intricate detail of host eggs (Spottiswoode and Stevens 2010). A crucial difference between this form of parasitic variation and host-specific parasitic variation (gentes) is that host-specific imprinting is unavailable as a mechanism through which parasites can target hosts with matching phenotypes. One alternative mechanism is that parasites could learn the appearance of their own eggs and seek out hosts of similar appearance. While common cuckoos have been cautiously suggested to single out reed warbler clutches better matching their own (Cherry et al. 2007b; Avilés et al. 2006a), in field studies it is difficult to exclude fully the possibility that ill-matched cuckoo eggs have been rejected by hosts prior to being found (Avilés et al. 2006a; Swynnerton 1918). Observations from other more phenotypically variable systems would seem to argue against parasites targeting particular individual phenotypes within a host species, at least with any degree of accuracy, despite the advantages this would confer: strikingly mismatched parasitic eggs are common in diderik cuckoos parasitizing masked weavers *Ploceus velatus* (Hunter 1961; Reed 1968), cuckoo finches parasitizing tawny-flanked prinias (Spottiswoode and Stevens 2010), and African cuckoos parasitizing fork-tailed drongos (C.N.S. and J.F.R. Colebrook-Robjent, unpubl. data); in the latter two cases parasites are known to incur heavy losses through host rejection. Thus in these cases parasites seem to lay their eggs haphazardly, relying on chance matches to succeed; this underscores the effectiveness of high degrees of phenotypic variability as a host defense.

Irrespective of whether or not parasites are able to deploy their eggs in a targeted manner when

faced with a polymorphic adversary, the highest fitness pay-offs should be gained by parasites that mimic whichever host phenotypes are commonest (Victoria 1972; Lively and Dybdahl 2000). Thus negative frequency-dependent selection might be expected to favor rare host egg phenotypes. Potential coevolutionary outcomes of such host defenses have been modeled theoretically (Takasu 2003; Takasu 2005), and found to depend on the starting distributions of host and parasitic phenotypes within the population, and the mode of inheritance of egg appearance. Possible outcomes are host and parasite egg phenotypes settling to a stable monomorphism; settling to a stable polymorphism; or continuously oscillating owing to hosts being able always to destabilize mimicry by parasites by evolving new phenotypes, in a close analogy of "Red Queen" dynamics (Van Valen 1973). The last-mentioned is expected when egg appearance is inherited autosomally, and when within-population variance in egg phenotype is greater in hosts than in parasites (Takasu 2005).

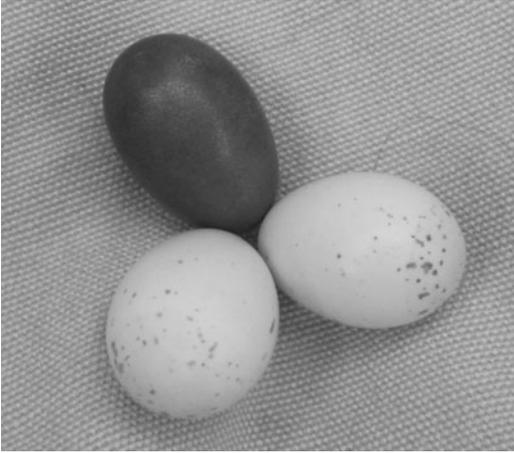
This raises the intriguing possibility that continuous arms races in egg appearance might result, under conditions that are likely to be realistic for many systems: first, while the mode of inheritance of egg appearance is still poorly understood, some of the few existing case studies have clearly shown an autosomal rather than maternal mode of inheritance (see Fossøy et al. 2010 for a recent review), which we might speculate could itself be the outcome of selection for diverse egg phenotypes. Second, greater variance in host versus parasitic phenotypes (of the appropriate gens) is not implausible and has been shown in at least one parasitic system, the cuckoo finch and its main host the tawny-flanked prinia (Spottiswoode and Stevens, in press). A temporal comparison of cuckoo finch and tawny-flanked prinia eggs over four decades has indeed showed patterns consistent with this prediction: prinia eggs became more diverse in color over time, as did cuckoo finch eggs (Spottiswoode and Stevens, in press). Thus, there is some evidence that visual trickery by brood parasites can result in "chase-away" selection on hosts, in some cases generating extreme levels of phenotypic variation used by hosts as signals of identity.

Effective signals of individual identity across the animal kingdom are predicted to be comprised of multiple uncorrelated characters, since this increases the information content of the signal by maximizing variability amongst individuals (Dale et al. 2001; Beecher 1982). Eggs should be no exception, and recent progress in devising methods to quantify independent aspects of egg appearance, including both color and pattern, has allowed this to be investigated quantitatively. Color, luminance, and five aspects of egg pattern show generally very low levels of correlation with one another in the hosts of the cuckoo finch (Spottiswoode and Stevens 2011). Ideally, this would be compared with background levels of correlation amongst egg traits in species with no history of interactions with brood parasites. Nonetheless, these results do point towards egg phenotypes as complex and multifaceted signals of identity, much as the complicated markings on bank-note watermarks render them more difficult to forge by counterfeiters. Taken together, the foregoing examples of counter-defenses involving egg variability argue that visual trickery can also be deployed in return by hosts to their own advantage.

Could parasites use visual trickery in ways other than mimicry alone to aid acceptance of parasitic eggs? This is an interesting question, not least since it may shed light on some of the numerous paradoxical examples of hosts failing to evolve egg discrimination (and hence parasites failing to evolve mimicry) despite the catastrophically high costs of parasitism they incur from blithely accepting parasitic eggs (reviewed by Davies 1999). To date, two non-mimetic visual tricks have been proposed. The first is to evade detection by becoming “invisible” to the host. This tactic is analogous to the “chemical insignificance” of insect brood parasites (Kilner and Langmore 2011), which foil detection based on pheromonal cues by reducing the complexity of their hydrocarbon signature (Lenoir et al. 2001). Several species of *Chalcites* cuckoos appear to evade host detection in a similar way. These cuckoos parasitize hosts that build dark, dome-shaped nests (Langmore et al. 2009b) and lay eggs that are an unusual olive green or bronze color, quite unlike the white speckled eggs of their hosts (Fig. 6.3). Visual modeling revealed that, in the eyes of the

host, the dense, dark pigment reduces the reflectance of the egg to a level similar to that of the nest lining (Langmore et al. 2009b), rendering the eggs cryptic to the host when viewed within the nest. Taken together with the finding that dark egg color is a derived trait in this lineage and occurs only in those species that parasitize dome-nesters exclusively, this strongly suggests that egg color in these *Chalcites* cuckoos has arisen through selection for crypsis (Langmore et al. 2009b). Cryptic eggs appear to be a highly successful tactic for avoiding detection by hosts, because hosts do not reject cryptic cuckoo eggs unless they are laid before the host has commenced laying (N. E. Langmore and G. Maurer unpublished data; Brooker and Brooker 1989; Langmore et al. 2009b; Sato et al. 2010; Tokue and Ueda 2010). Crypsis should have several advantages over mimicry as a form of visual trickery, not least that it should allow parasites to exploit more than one dark-nesting host species without acquiring host-specific adaptations, and to colonize a new host species that has already evolved egg rejection (Brooker et al. 1990; Langmore et al. 2009b). These advantages might suggest that it could be more widespread a parasitic strategy than currently appreciated. Might crypsis help to account for other striking examples of parasitic mismatch in the relatively bright light environment of open-nesting hosts (e.g., common cuckoo vs. dunnoek *Prunella modularis*, or red-chested cuckoo vs. cape robin-chat *Cossypha caffra*)? These questions remain to be investigated using the appropriate visual models and, ideally, field experiments.

A second form of non-mimetic visual trickery by parasites is visual superstimulus. Birds in general may have sensory predispositions to certain phenotypes: for example, herring gulls *Larus argentatus* prefer artificial eggs that are larger and greener than their own, and marked with relatively fine and contrasting speckles (Baerends and Drent 1982). Could brood parasites “charm” their hosts by producing eggs (or chicks, e.g., Soler et al. 1995a) with similarly exaggerated traits that are visually attractive to hosts, rather than perfectly mimetic? Three observations from rufous bush-robins *Cercotrichas galactotes* suggest that hosts might be susceptible to this form of trickery: in bush-robins, model eggs that resem-



**Figure 6.3** The cryptic egg of a shining bronze-cuckoo *Chalcites lucidus* with two eggs of its host, a yellow-rumped thornbill *Acanthiza chrysorrhoa* (photo: Naomi Langmore). See also Plate 11.

bled neither those of their corresponding gens of cuckoo (which is imperfectly mimetic) nor their own were just as likely to be accepted as perfectly mimetic experimental eggs, whereas eggs with partial mimicry were usually rejected (Alvarez 1999). This suggests that visual traits of the non-mimetic experimental eggs (which were either whiter, or had more contrasting markings) aided their acceptance. Moreover, identically painted model eggs were more likely to be accepted if they were larger than either bush-robin eggs, or cuckoo eggs of the bush-robin gens (Alvarez 2000). Similar results with respect to both color and size have also been found in European magpies *Pica pica* parasitized by the great spotted cuckoo *Clamator glandarius* (Alvarez et al. 1976), and in both cuckoo species real cuckoo eggs differ from host eggs in accordance with this apparent host preference, being larger, paler, and with more contrasting markings. New methods for quantifying independent components of egg appearance (including both pattern and color) should make future analyses of this kind even more powerful. While the hypothesis that blue-green egg colors are attractive to birds as sexual signals remains controversial (Moreno and Osorno 2003; reviewed by Reynolds et al. 2009), it does suggest one avenue through which brood parasites might exploit pre-existing host preferences to their own advantage.

Finally, egg mimicry should evolve when parasites impose strong fitness costs on hosts, and thus selection for egg recognition, and we began this section by mentioning an exception. The one brood parasitic group (although it comprises just one species) in which egg mimicry has not evolved, the black-headed duck, would at first sight seem to be perfectly consistent with this prediction: owing to its highly precocial young it imposes negligible fitness costs on hosts, and lays unmarked whitish eggs that contrast strikingly with the mottled eggs of its favorite hosts, two species of coot (*Fulica* spp.) (Weller 1968). But a paradox arises because coots do regularly discriminate strongly against mismatched eggs, resulting in high fitness costs for the duck. In this instance egg rejection behavior has been suggested to be the product of defenses against intraspecific brood parasitism between coot females, in which the duck now appears to find itself trapped and unable to evolve its way out owing to strong selection by hosts against even partially mimetic eggs (Lyon and Eadie 2004). An intriguing alternative may be that the parasitic duck egg's lack of mimicry serves to signal to the hosts "I am a duck egg," and therefore harmless in comparison to a coot chick requiring parental care and not worth the potential costs of ejecting (N. B. Davies, pers. comm.).

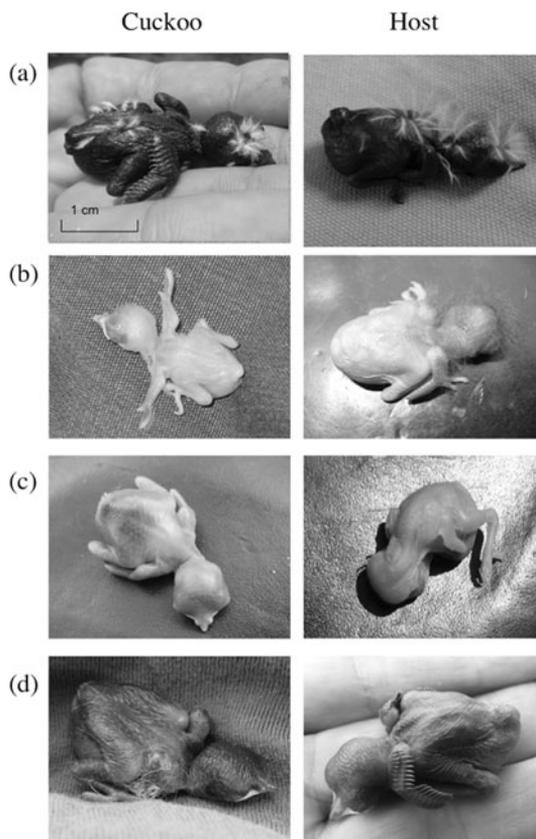
## 6.4 The nestling stage

Brood parasitic nestlings are generally more renowned for their lack of resemblance to host young than for mimicry. In contrast to the exquisite mimicry of host eggs by many brood parasites, brood parasitic chicks typically differ from host young in traits such as size, mouth color, skin color in naked chicks and plumage color in feathered chicks. The failure of many brood parasites to mimic host young appears to reflect the relative rarity of host defenses against parasitism at the nestling stage (Davies 2000). Most hosts attack an adult brood parasite near the nest, and many hosts reject foreign eggs in their nests, but rejection of brood parasitic chicks was, until recently, unknown.

The first evidence of cuckoo nestling rejection by hosts came from a study of the superb fairy-wren

*Malurus cyaneus*, which is parasitized by Horsfield's bronze-cuckoo *Chalcites basalis* (Langmore et al. 2003). Over a third of host parents abandon the young cuckoo a few days after hatching, leaving it to die in the nest. More recently, cuckoo nestling rejection has also been documented in other bronze-cuckoo hosts; cuckoo chick rejection by eviction from the nest was discovered in two hosts of the little bronze-cuckoo *C. minutillus*; the large-billed gerygone *Gerygone magnirostris* (Sato et al. 2010); and the mangrove gerygone *G. laevigaster* (Tokue and Ueda 2010); and there is also some indication of shining cuckoo *Chalcites lucidus* chick discrimination in the grey warbler *G. igata* (McLean and Maloney 1998). Just as cuckoo egg rejection by hosts has selected for egg mimicry in cuckoos, we might expect that cuckoo chick rejection by these hosts would select for chick mimicry in cuckoos. A recent study confirms just that; the chicks of three species of bronze-cuckoos are striking visual mimics of their morphologically diverse hosts (Fig. 6.4; Langmore et al. 2011). This study uses recent models of avian visual processing to demonstrate that the cuckoo nestlings resemble host young, not only through human eyes, but also in the eyes of the hosts themselves. The nestling cuckoos mimic their hosts in the color of their skin and rictal flange (the broad, colorful border of the nestling mouth), as well as in the incidence of natal down. One cuckoo species even expresses a derived trait that mimics that of their hosts; nestlings of the little bronze-cuckoo (*C. m. minutillus*) display multi-barbed "fluffy" natal down (Langmore et al. 2011), which is typical of nestling passerines but unique amongst cuckoos (Payne 1977).

The bronze-cuckoos appear to track variation in host nestling morphology with remarkable accuracy, even down to the level of subspecies (Table 6.2). For example, northern Australian hosts of the little bronze-cuckoo typically display dark skin and white natal down at the nestling stage, which is mimicked by the cuckoo (Fig. 6.4 Langmore et al. 2011; Sato et al. 2010; Tokue and Ueda 2010). However, the more southerly host, the white-throated gerygone *G. albobularis*, displays pink skin and yellow down. This host is parasitized by a subspecies of the little bronze-cuckoo, *C. m. barnardi*, which also displays pink skin and yellow down



**Figure 6.4** Visual mimicry of host chicks by nestling *Chalcites* cuckoos. a) Little bronze-cuckoo *C. minutillus* and large-billed gerygone *Gerygone magnirostris*; b) Shining bronze-cuckoo *C. lucidus* and yellow-rumped thornbill *Acanthiza chrysorrhoa*; c) Horsfield's bronze-cuckoo and superb fairy-wren *Malurus cyaneus*; d) Horsfield's bronze-cuckoo and purple-crowned fairy-wren *M. coronatus* (from Langmore, NE, Stevens, M, Maurer, G, Heinsohn, R, Hall, ML, Peters, A, Kilner, RM (2011) Visual mimicry of host nestlings by cuckoos. *Proceedings of the Royal Society: Biological Sciences*, 278: 2455–2463. Photos: Naomi Langmore, Golo Maurer, Michelle Hall). See also Plate 12.

(McGill and Goddard 1979, Table 6.2). The morphological differences between the different subspecies of these bronze-cuckoo species are markedly more pronounced as nestlings than as adults.

Experiments suggest that the high fidelity of bronze-cuckoo nestling mimicry is adaptive and has arisen through coevolution with their hosts. The superb fairy-wren is a primary host of Horsfield's bronze-cuckoo and an infrequent host of the shining bronze-cuckoo. Horsfield's bronze-cuckoo chicks (pink and grey skin; white flange) are

**Table 6.2** Subspecies of *Chalcites* cuckoos mimic their morphologically diverse hosts.

Cuckoo nestling	Host nestling
<b>Little bronze-cuckoo</b> <i>C. m. barnardi</i> <sup>1</sup> Pink skin ? rictal flange Pale yellowish down	<b>White-throated gerygone</b> <i>Gerygone olivacea</i> <sup>1, 2</sup> Pink skin White rictal flange Pale yellowish down
<b>Little bronze-cuckoo</b> <i>C. m. minutillus</i> <sup>3</sup> Black skin Greenish-white rictal flange Multi-barbed white down	<b>Large-billed gerygone</b> <i>Gerygone magnirostris</i> <sup>3</sup> Black skin Greenish-white rictal flange Multi-barbed white down
<b>Shining bronze-cuckoo</b> <i>C. l. plagosus</i> <sup>3</sup> Yellow skin Yellow rictal flange Sparse or no down	<b>Yellow-rumped thornbill</b> <i>Acanthiza chrysorhoa</i> <sup>3</sup> Yellow skin Yellow rictal flange Fine grey down
<b>Shining cuckoo</b> <i>C. l. lucidus</i> <sup>4, 5</sup> Pink and grey skin White rictal flange, becomes yellow Sparse white hair-like down	<b>Grey warbler</b> <i>Gerygone igata</i> <sup>5, 6</sup> Pink or grey skin White rictal flange, becomes yellow Abundant white down

References: <sup>1</sup> McGill and Goddard 1979, <sup>2</sup> Pers. obs. <sup>3</sup> Langmore et al. 2011; <sup>4</sup> Gill 1982; <sup>5</sup> Gill 1998; <sup>6</sup> Anderson, M. pers. comm.

more similar than shining bronze-cuckoo chicks (yellow, or rarely black skin; yellow flange) to their fairy-wren hosts (pink skin; white flange) (Fig. 6.4 Langmore et al. 2011). Cross-fostering experiments, in which cuckoos were transferred into superb fairy-wren nests at the egg stage, revealed that shining bronze-cuckoo chicks were rejected by superb fairy-wrens at a significantly higher rate (100%) than Horsfield's bronze-cuckoo chicks (40%, Langmore et al. 2003).

A close resemblance has also been reported between two non-evicting brood parasites and their hosts. Great spotted cuckoo nestlings appear (to human eyes, at least) to be similar to host young (Lack 1968). This resemblance has been attributed to low variation in altricial nestling appearance (Grim 2005; Soler et al. 1995b), but it is also plausible that it has evolved in response to host defenses. Cross-fostering experiments revealed that host magpies reject some nestlings of other species that are placed in their nests, as well as rejecting some of their own young when their skin or plumage was dyed (Alvarez et al. 1976). Mimicry of host young also occurs in screaming cowbirds *Molothrus*

*rufocollaris*, a specialist parasite of the bay-winged cowbird *M. badius*. Hosts do not discriminate against non-mimetic nestlings, but they do show discrimination against non-mimetic fledglings (Fraga 1998). Correspondingly, the parasite does not mimic host nestling skin color (Fraga 1998; but see Lichtenstein, 2001), but shows precise mimicry of host plumage as a dependent fledgling (Fraga 1998). A similarity between parasite and host young has also been reported in several other host-parasite systems (reviewed in Davies and Brooke 1988b; Grim 2006), but it is unknown whether these have evolved as a result of host-parasite interactions or through some other process (e.g. common ancestry, predator avoidance; reviewed in Grim 2005).

The precise mimicry shown by some young cuckoos and cowbirds is at odds with the perception that brood parasite chicks generally fail to mimic their hosts (Rothstein and Robinson 1998). Why is chick mimicry necessary to fool some hosts but not others? Lotem (1993) proposed a convincing explanation for the failure of many hosts to discriminate parasite chicks through learning. He demonstrated

that the high cost of misimprinting on a cuckoo nestling and subsequently rejecting all future host offspring should prevent the evolution of learned chick recognition. Similarly, among hosts of non-evicting parasites learned recognition of brood parasite chicks is only likely to evolve under a relatively rare suite of conditions: when host chick survival in parasitized nests is low, rates of parasitism are high and clutch size is large (Lawes and Marthews 2003). Further, some non-evicting parasites carry a lower cost to hosts than evicting parasites, and may not depress host reproductive success sufficiently to outweigh the costs of nestling recognition errors.

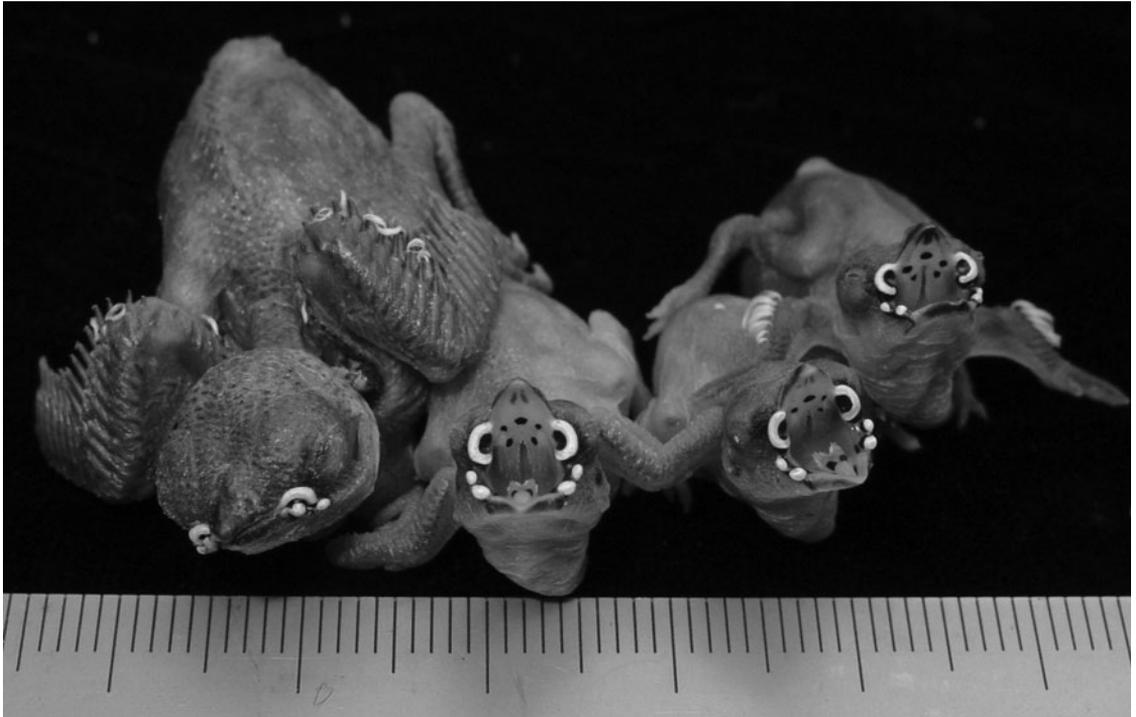
Despite the solid theoretical basis for dismissing the possibility of learned nestling recognition, a subsequent study demonstrated that learning can indeed facilitate discrimination of parasite chicks, if used in conjunction with other mechanisms for discrimination that decrease the probability of misimprinting. Superb fairy-wrens optimize chick rejection decisions by integrating learned recognition cues and external cues (Langmore et al. 2009a). Females only reject chicks that are alone in the nest, and only when adult cuckoos are present in the area, thereby greatly reducing the possibility of making a recognition error. Further, experienced breeders are both more likely both to reject a lone cuckoo chick and accept a lone fairy-wren chick than naïve females, indicating that rejection decisions improve with breeding experience.

An alternative explanation for the lack of chick discrimination in many hosts is that the success of earlier lines of defense against parasitism (e.g., mobbing, egg rejection) may result in diminishing returns from a later line of defense (Britton et al. 2007; Dawkins and Krebs 1979; Grim 2006; Planque et al. 2002). For example, if mobbing successfully foils most attempts at parasitism, a parasite egg or chick in the nest may be such a rare event that the benefits of evolving rejection behavior are outweighed by rejection costs (e.g., Krüger 2011). This could explain the variability between hosts in the elaboration of defense portfolios, and thereby explain the corresponding variability between brood parasites in the evolution of mimicry to circumvent host defenses.

## 6.5 Visual trickery to elicit parental care

Brood parasitic nestlings face a twofold challenge in the nests of their hosts; not only must they circumvent any host recognition systems (Section 6.4 above), but they must also provide the appropriate signals to stimulate provisioning by their hosts. To do so requires exploiting the parent–offspring communication system of the host species (Kilner and Davies 1999). The begging display of nestling birds typically comprises a combination of visual and vocal signals, including begging calls, posturing, and brightly colored gapes. Parents integrate these signals to adjust their provisioning rate to the hunger level of their brood (Kilner and Davies 1999).

In order to stimulate provisioning by the host, mimicry of host begging signals may be necessary. For example, the brood parasitic *Vidua* finches of Africa, which are reared alongside the host young, mimic the elaborate gape patterns of their estrildid finch hosts. Most *Vidua* species are specific to a single host species, and precisely match the distinctive gape pattern of that host (Fig. 6.5). The resemblance does not appear to have evolved in response to host defenses, because hosts fail to reject young with abnormal gape markings (Schuetz 2005a; Schuetz 2005b). However, when gape markings were obscured experimentally, nestlings suffered a reduced provisioning rate, suggesting that the markings provide a necessary stimulus to elicit provisioning by host parents (Schuetz 2005b). This experiment provides an elegant explanation for why gape mimicry has evolved, but it does not explain why gape patterns have diversified between host species. Recently, an intriguing hypothesis was put forward to explain this conundrum. Hauber and Kilner (2007) suggested that competition between parasite and host young for parental resources might lead to exaggeration of those aspects of the signal that most effectively exploit host parents. *Vidua* chicks are likely to experience stronger selection for exaggerated signals than host young, because they are unrelated to the other chicks in the nest and are therefore under selection to behave more selfishly (Lichtenstein 2001). However, as parasite chicks become more efficient



**Figure 6.5** Parasitic pin-tailed whydah *Vidua macroura* nestlings (the two outer chicks) are visual mimics of common waxbill *Estrilda astrild* nestlings (the two center chicks, photo: Justin Schuetz). See also Plate 13.

at monopolizing parental care, host young will likewise experience selection for exaggerated signals to allow them to compete effectively with parasites. Although the exaggeration of signals is likely to be constrained to remain below a certain threshold to ensure acceptance by the host (Holen et al. 2001), this scenario could ultimately result in a paradoxical situation in which host young evolve mimicry of parasite young (Hauber and Kilner 2007).

Brood parasites that are larger than their hosts face an additional challenge in acquiring sufficient resources from their host parents. Most cuckoo species are larger than their hosts, and some cuckoo chicks can grow to more than ten times the size of their foster parents (Davies 2000). Therefore a cuckoo chick requires more food than a single host chick, yet it can display only one gape and the begging call of one individual. How then do parasitic chicks ensure that host parents provide them with

sufficient food? Studies on two species of cuckoo reveal ingenious solutions to this problem.

The common cuckoo is reared alone in the nest, yet the rate at which the host parents feed the cuckoo chick is similar to the rate at which they provision a brood of four of their own chicks (Kilner and Davies 1999). The cuckoo chick solicits such a high rate of care partly by exploiting the tendency of its reed warbler hosts to vary provisioning rate in relation to the total area of nestling gapes presented during a nest visit. By presenting a relatively large gape to its foster parents, the cuckoo can solicit a greater rate of care than a single host chick. However, this alone does not elicit sufficiently high provisioning rates, and the cuckoo supplements its larger gape by producing an extremely rapid begging call, which simulates the sounds produced by four host nestlings (Kilner and Davies 1999).



**Figure 6.6** The Horsfield's hawk-cuckoo reveals a bare wing patch during its begging display to simulate multiple begging mouths and thereby drive its foster parents to greater provisioning efforts. In this photo, the host is thoroughly fooled, and tries to place food in the wing patch (photo: Keisuke Ueda).

The Horsfield's hawk-cuckoo *Cuculus fugax* of south-east Asia has come up with a different solution to the challenge of eliciting sufficient care from its hosts. During the begging display, the cuckoo chick raises its wing to reveal a naked skin patch under the wing, which mimics the appearance of a nestling gape (Fig. 6.6; Tanaka and Ueda 2005). The wing patch is displayed at a greater rate when the provisioning rate of the foster parents is slow. The hosts are apparently fooled by the wing patch, because they sometimes try to place food in the wing patch rather than the gape (Fig. 6.6), and because experimental darkening of the wing patch results in a reduced provisioning rate (Tanaka and Ueda 2005). These two studies cleverly illustrate how cuckoos have evolved the ability to solicit sufficient care by tuning into the sensory predispositions of their hosts.

## 6.6 Mimicry in generalist versus specialist parasites

Mimicry of hosts is a more challenging feat for a generalist parasite than a specialist. Generalists parasitize several different host species, each of which may display distinct egg and chick morphologies. Some types of signals can be modified after parasitism to resemble the appropriate host species. For example, nestling Horsfield's bronze-cuckoos can modify their begging calls to mimic those of the host species that rears them (Langmore et al. 2008).

Similarly, insect brood parasites may acquire the colony-specific hydrocarbon signature of their host after parasitism (Kilner and Langmore 2011; Lenoir et al. 2001). However, visual signals generally lack the phenotypic plasticity necessary for modification after parasitism. Instead, generalist brood parasites have come up with two alternative solutions to the problem of mimicking morphologically diverse hosts.

First, brood parasites may evolve host-specific gentes, each of which produces progeny that matches that of its favored host. For example, as discussed earlier (Section 6.3) several cuckoo species (as well as, independently, the cuckoo finch) have evolved gentes, each of which lays an egg that matches that of its host. Host-specific races can be maintained as a single species where there are cross-matings of males with females of different gentes, as has been described in the common cuckoo (Gibbs et al. 2000) and greater honeyguide (Spottiswoode et al. 2011), or they can diverge into separate species where there is assortative mating between males and females of the same gens. The latter process appears to account for the remarkably rapid speciation of *Vidua* finches, which not only resemble their specialist hosts with respect to chick mouth markings, but are exceptional in that both sexes imprint on their respective hosts' songs (males mimic them and females are attracted to them); thus instant host-specific reproductive isolation and speciation can result (Sorenson et al. 2003). In common

cuckoos, evidence for a degree of assortative mating according to host origin has also been found on a local scale (Fossøy et al. 2010), which if widespread and consistent may represent the beginnings of such a process. Likewise, we can speculate that diversifying selection driven by host discrimination of cuckoo chicks (and consequent selection for cuckoo mimicry of host chicks) could explain the diversity of species and subspecies of *Chalcites* cuckoos (Langmore et al. 2011). Thus selection on cuckoos for mimicry of host eggs and chicks could explain recent evidence that species richness is higher in parasitic than non-parasitic cuckoos (Krüger et al. 2009).

Second, generalist parasites may adopt a morphology that is intermediate between that of several hosts ("imperfect mimicry," Sherratt 2002). This strategy appears to have been adopted by the common cuckoo in addition to evolving gentes. Each gens lays an egg that matches its favored host, but the eggs display more "average" markings than host eggs, perhaps to facilitate parasitism of subsidiary hosts (Stoddard and Stevens 2010). Similarly, the Horsfield's bronze-cuckoo, which is the most generalist of the Australian bronze-cuckoos, produces nestlings that are intermediate in color between their various host species (Langmore et al. 2011). The nestlings display pink skin on the upper back, and grey skin on the head and lower back, thereby achieving a moderate resemblance to both light and dark skinned host species (Langmore et al. 2011). Imperfect mimicry may carry a cost to the parasite, because generalist Horsfield's bronze-cuckoo nestlings in superb fairy-wren nests tend to suffer a higher rejection rate (38%, Langmore et al. 2003) than the specialist shining bronze-cuckoo in yellow-rumped thornbill nests (0%, Langmore unpublished data) or the specialist little bronze-cuckoo in mangrove gerygone (18%, Tokue and Ueda 2010) or large-billed gerygone nests (36%, Sato et al. 2010).

## 6.7 Conclusions

The dazzling array of visual tricks displayed by brood parasites to manipulate their hosts has evolved through two processes: either as a coevolu-

tionary response to host defenses against brood parasites, or to "tune in" to pre-existing host provisioning strategies. Davies (2011) terms these two processes "trickery" and "tuning." The most common form of visual trick selected by both processes is mimicry, which has evolved at all three stages of the parasitic process: gaining access to host nests, the egg stage, and the chick stage (Welbergen and Davies, 2011). Aggressive mimicry, in which the predatory or parasitic species mimics a harmless or inviting species in order to gain access to resources (Ruxton et al. 2004), is the most common form of mimicry in brood parasites, but Batesian mimicry, in which a defenseless species mimics a harmful one, also occurs in the case of hawk mimicry by common cuckoos (Welbergen and Davies 2011). The special case of parasite "tuning" into host provisioning strategies has given rise to additional visual tricks in the form of supernormal stimuli, such as large or false gapes. In general, trickery and tuning have different impacts on host populations. Trickery evolves in response to host defenses and usually provokes reciprocal genetic change in host populations, as they evolve counter-adaptations to cuckoo tricks (e.g., Lahti 2005; Langmore et al. 2003; Spottiswoode and Stevens, in press; Yang et al. 2010). By contrast, tuning allows the parasite to exploit pre-existing host provisioning strategies and does not typically lead to reciprocal adaptations in hosts (but see Hauber and Kilner 2007). The recent technological advances that allow quantification of mimicry through the eyes of the host have provided us with fascinating insights into the exquisite subtlety of visual trickery in brood parasites. They also pave the way for future research into the relatively less well-understood reciprocal adaptations of host populations in response to the visual tricks of brood parasites.

## Acknowledgements

We thank Nick Davies and Justin Welbergen for helpful comments on the manuscript, and Roy and Marie Battell, Steve Grimwade, Michelle Hall, Golo Maurer, Justin Schuetz, Keisuke Ueda, and Jack Wolf for providing photographs. NEL was supported by an Australian Research Council Australian Research Fellowship. CNS was supported by a

Royal Society Dorothy Hodgkin Fellowship and the DST/NRF Centre of Excellence at the Percy FitzPatrick Institute, University of Cape Town.

## References

- Alvarez, F. (1999). Attractive non-mimetic stimuli in Cuckoo *Cuculus canorus* eggs. *Ibis* **141**, 142–144.
- Alvarez, F. (2000). Response to Common Cuckoo *Cuculus canorus* model egg size by a parasitized population of Rufous Bush Chat *Cercotrichas galactotes*. *Ibis* **142**, 683–686.
- Alvarez, F., Arias De Reyna, L., and Segura, M. (1976). Experimental brood parasitism of the magpie (*Pica pica*). *Animal Behaviour* **24**, 907–916.
- Avilés, J. M. (2008). Egg colour mimicry in the common cuckoo *Cuculus canorus* as revealed by modelling host retinal function. *Proceedings of the Royal Society of London B* **275**, 2345–2352.
- Avilés, J. M., Stokke, B. G., Moksnes, A., Røskaft, E., Asmul, M., and Møller, A. P. (2006a). Rapid increase in cuckoo egg matching in a recently parasitized reed warbler population. *Journal of Evolutionary Biology* **19**, 1901–1910.
- Avilés, J. M., Stokke, B. G., Moksnes, A., Røskaft, E., and Møller, A. P. (2006b). Nest predation and the evolution of egg appearance in passerine birds in Europe and North America. *Evolutionary Ecology Research* **8**, 493–513.
- Baerends, G. P. and Drent, R. H. (1982). The herring gull and its egg. Part II. The responsiveness to egg features. *Behaviour* **82**, 1–416.
- Beecher, M. D. (1982). Signature systems and kin recognition. *American Zoologist*, **22**, 477–490.
- Britton, N. F., Planque, R., and Franks, N. R. (2007). Evolution of defence portfolios in exploiter-victim systems. *Bulletin of Mathematical Biology* **69**, 957–988.
- Brooke, M. de L. and Davies, N. B. (1988). Egg mimicry by cuckoos *Cuculus canorus* in relation to discrimination by hosts. *Nature* **335**, 630–632.
- Brooker, M. G. and Brooker, L. C. (1989). The comparative breeding behaviour of two sympatric cuckoos, Horsfield's bronze-cuckoo *Chrysococcyx basalus* and the shining bronze-cuckoo *C. lucidus*, in Western Australia: a new model for the evolution of egg morphology and host specificity in avian brood parasites. *Ibis* **131**, 528–547.
- Brooker, L. C., Brooker, M. G., and Brooker, A. M. H. (1990). An alternative population/genetics model for the evolution of egg mimesis and egg crypsis in cuckoos. *Journal of Theoretical Biology* **146**, 123–143.
- Cassey, P., Honza, M., Grim, T., and Hauber, M. E. (2008). The modelling of avian visual perception predicts behavioural rejection responses to foreign egg colours. *Biology Letters* **4**, 515–517.
- Cherry, M. I. and Bennett, A. T. D. (2001). Egg colour matching in an African cuckoo, as revealed by ultraviolet-visible reflectance spectrophotometry. *Proceedings of the Royal Society of London B* **268**, 565–572.
- Cherry, M. I., Bennett, A. T. D., and Moskát, C. (2007a). Host intra-clutch variation, cuckoo egg matching and egg rejection by great reed warblers. *Naturwissenschaften* **94**, 441–447.
- Cherry, M. I., Bennett, A. T. D., and Moskát, C. (2007b). Do cuckoos choose nests of great reed warblers on the basis of host egg appearance? *Journal of Evolutionary Biology* **20**, 1218–1222.
- Craib, J. (1994). Why do common cuckoos resemble raptors? *British Birds* **87**, 78–79.
- Dale, J., Lank, D. B., and Reeve, H. K. (2001). Signaling individual identity versus quality: a model and case studies with ruffs, queleas, and house finches. *American Naturalist* **158**, 75–86.
- Davies, N. B. (1992). *Dunmock Behaviour and Social Evolution*. Oxford University Press, Oxford.
- Davies, N. B. (1999). Cuckoos and cowbirds versus hosts: co-evolutionary lag and equilibrium. *Ostrich* **70**, 71–79.
- Davies, N. B. (2011). Cuckoo adaptations: trickery and tuning. *Journal of Zoology* **284**, 1–14.
- Davies, N. B. and Brooke, M. de L. (1988). Cuckoos versus reed warblers: adaptations and counteradaptations. *Animal Behaviour* **36**, 262–284.
- Davies, N. B. and Brooke, M. de L. (1989a). An experimental study of co-evolution between the cuckoo, *Cuculus canorus*, and its hosts. I. Host egg discrimination. *Journal of Animal Ecology* **58**, 207–224.
- Davies, N. B. and Brooke, M. de L. (1989b). An experimental study of co-evolution between the cuckoo, *Cuculus canorus*, and its hosts. II. Host egg markings, chick discrimination and general discussion. *Journal of Animal Ecology* **58**, 225–236.
- Davies, N. B. and Welbergen, J. A. (2008). Cuckoo-hawk mimicry? An experimental test. *Proceedings of the Royal Society of London B* **275**, 1817–1822.
- Dawkins, R. and Krebs, J. R. (1979). Arms races between and within species. *Proceedings of the Royal Society of London B* **205**, 489–511.
- Dominey, W. J. (1980). Female mimicry in male bluegill sunfish—a genetic polymorphism? *Nature* **284**, 546–548.
- Dumbacher, J. P. and Fleischer, R. C. (2001). Phylogenetic evidence for colour pattern convergence in toxic pit-

- huis: Müllerian mimicry in birds? *Proceedings of the Royal Society of London B* **268**, 1971–1976.
- Endler, J. A. and Mielke, P. W. J. (2005). Comparing color patterns as birds see them. *Biological Journal of the Linnean Society* **86**, 405–431.
- Fossøy, F., Antonov, A., Moksnes, A., Røskaft, E., Vikan, J. R., Møller, A. P., Shykoff, J. A., and Stokke, B. G. (2010). Genetic differentiation among sympatric cuckoo host races: males matter. *Proceedings of the Royal Society of London B* **278**, 1639–1645.
- Fraga, R. M. (1985). Host-parasite interactions between Chalk-browed Mockingbirds and Shiny Cowbirds. *Ornithological Monographs* **36**, 829–844.
- Fraga, R. M. (1998). Interactions of the parasitic screaming and shiny cowbirds (*Molothrus rufoaxillaris* and *M. bonariensis*) with a shared host, the bay-winged cowbird (*M. badius*). In: *Parasitic Birds and their Hosts* (eds Rothstein, S.I. and Robinson, S.K.) Oxford University Press, Oxford.
- Gibbs, H. L., Sorenson, M. D., Marchetti, K., Brooke, M. D., Davies, N. B., and Nakamura, H. (2000). Genetic evidence for female host-specific races of the common cuckoo. *Nature* **407**, 183–186.
- Gill, B. J. (1982). Notes on the shining cuckoo (*Chrysococcyx lucidus*) in New Zealand. *Notornis* **29**, 215–227.
- Gill, B. J. (1988). Behaviour and ecology of the shining cuckoo, *Chrysococcyx lucidus*. In: *Parasitic Birds and their Hosts* (eds Rothstein, S. I. and Robinson, S. K.) Oxford University Press, Oxford.
- Grim, T. (2005). Mimicry vs. similarity: which resemblances between brood parasites and their hosts are mimetic and which are not? *Biological Journal of the Linnean Society* **84**, 69–78.
- Grim, T. (2006). The evolution of nestling discrimination by hosts of parasitic birds: why is rejection so rare? *Evolutionary Ecology Research* **8**, 785–802.
- Harper, G. R. and Pfenning, D. W. (2008). Selection overrides gene flow to break down maladaptive mimicry. *Nature* **451**, 1103–1106.
- Hauber, M. E. and Kilner, R. M. (2007). Coevolution, communication and host-chick mimicry in parasitic finches: who mimics whom? *Behavioural Ecology and Sociobiology* **61**, 497–503.
- Higuchi, H. (1989). Responses of the bush warbler *Cettia diphone* to artificial eggs of *Cuculus* cuckoos in Japan. *Ibis* **131**, 94–98.
- Holen, O. H., Saetre, G.-P., Slagsvold T., and Stenseth, N. C. (2001). Parasites and supernormal manipulation. *Proceedings of the Royal Society of London B* **268**, 2551–2558.
- Honza, M., Kuiper, S. M., and Cherry, M. I. (2005). Behaviour of African turdid hosts towards experimental parasitism with artificial red-chested cuckoo *Cuculus solitarius* eggs. *Journal of Avian Biology* **36**, 514–522.
- Hunter, H. C. (1961). Parasitism of the Masked Weaver *Ploceus velatus arundinaceus*. *Ostrich* **32**, 55–63.
- Jackson, W. M. (1998). Egg discrimination and egg-color variability in the northern masked weaver: the importance of conspecific versus interspecific parasitism. In: *Parasitic Birds and their Hosts* (eds Rothstein, S. I. and Robinson, S. K.) Oxford University Press, Oxford.
- Johnsgard, P. A. (1997). *The Avian Brood Parasites: Deception at the Nest*, Oxford University Press, Oxford.
- Kilner, R. M. (2006). The evolution of egg colour and patterning in birds. *Biological Reviews* **81**, 383–406.
- Kilner, R. M. and Davies, N. B. (1999). How selfish is a cuckoo chick? *Animal Behaviour* **58**, 797–808.
- Kilner, R. M. and Langmore, N. E. (2011). Cuckoos versus hosts in insects and birds: adaptations, counter-adaptations and outcomes. *Biological Reviews* **86**, 836–852.
- Krüger, O. (2011). Brood parasitism selects for no defence in a cuckoo host. *Proceedings of the Royal Society of London B* **278**, 2777–2783.
- Krüger, O., Davies, N. B., and Sorenson, M. D. (2007). The evolution of sexual dimorphism in parasitic cuckoos: sexual selection or coevolution? *Proceedings of the Royal Society of London B* **274**, 1553–1560.
- Krüger, O., Sorenson, M. D., and Davies, N. B. (2009). Does coevolution promote species richness in parasitic cuckoos? *Proceedings of the Royal Society of London B* **276**, 3871–3879.
- Lack, D. (1968). *Ecological Adaptations for Breeding in Birds*. Methuen & Co. Ltd, London.
- Lahti, D. C. (2005). Evolution of bird eggs in the absence of cuckoo parasitism. *Proceedings of the National Academy of Sciences USA* **102**, 18057–18062.
- Lahti, D. C. (2006). Persistence of egg recognition in the absence of cuckoo brood parasitism: pattern and mechanism. *Evolution* **60**, 157–168.
- Lahti, D. C. and Lahti, A. R. (2002). How precise is egg discrimination in weaverbirds? *Animal Behaviour* **63**, 1135–1142.
- Landstrom, M. T., Heinsohn, R., and Langmore, N. E. (2010). Clutch variation and egg rejection in three hosts of the pallid cuckoo, *Cuculus pallidus*. *Behaviour* **147**, 19–36.
- Langmore, N. E., Cockburn, A., Russell, A. F., and Kilner, R. M. (2009a). Flexible cuckoo chick-rejection rules in the superb fairy-wren. *Behavioral Ecology* **20**, 978–984.
- Langmore, N. E., Hunt, S., and Kilner, R. M. (2003). Escalation of a coevolutionary arms race through host rejection of brood parasitic young. *Nature* **422**, 157–160.
- Langmore, N. E. and Kilner, R. M. (2009). Why do Horsfield's bronze-cuckoo *Chalcites basalis* eggs mimic

- those of their hosts? *Behavioural Ecology and Sociobiology* **63**, 1127–1131.
- Langmore, N. E., Kilner, R. M., Butchard, S. H. M., Maurer, G., Davies, N. B., Cockburn, A., Macgregor, N. A., Peters, A., Magrath, M. J. L., and Dowling, D. (2005). The evolution of egg rejection by cuckoo hosts in Australia and Europe. *Behavioural Ecology* **16**, 686–692.
- Langmore, N. E., Maurer, G., Adcock G. J., and Kilner, R. M. (2008). Socially acquired host-specific mimicry and the evolution of host races in Horsfield's bronze-cuckoo *Chalcites basalis*. *Evolution* **62**, 1689–1699.
- Langmore, N. E., Stevens, M., Heinsohn, R., Hall, M. L., Peters, A., and Kilner, R. M. (2011). Visual mimicry of host nestlings by cuckoos. *Proceedings of the Royal Society of London B* **278**, 2455–2463.
- Langmore, N. E., Stevens, M., Maurer, G., and Kilner, R. M. (2009b). Are dark cuckoo eggs cryptic in host nests? *Animal Behaviour* **78**, 461–468.
- Lawes, M. J. and Marthens, T. R. (2003). When will rejection of parasite nestlings by hosts of nonvicting avian brood parasites be favored? A misimprinting-equilibrium model. *Behavioural Ecology* **14**, 757–770.
- Lenoir, A., D'Ettoir, P., and Errard, C. (2001). Chemical ecology and social parasitism in ants. *Annual Review of Entomology* **46**, 573–599.
- Lichtenstein, G. (2001). Low success of shiny cowbird chicks parasitizing rufous-bellied thrushes: chick-chick competition or parental discrimination? *Animal Behaviour* **61**, 401–413.
- Lively, C. M. and Dybdahl, M. F. (2000). Parasite adaptation to locally common host genotypes. *Nature* **405**, 679–681.
- Lotem, A. (1993). Learning to recognize nestlings is maladaptive for cuckoo *Cuculus canorus* hosts. *Nature* **362**, 743–745.
- Lyon, B. E. and Eadie, J. M. (2004). An obligate brood parasite trapped in the intraspecific arms race of its hosts. *Nature* **432**, 390–393.
- Mason, P. and Rothstein, S. I. (1987). Crypsis versus mimicry and the color of shiny cowbird eggs. *American Naturalist* **130**, 161–167.
- McGill, I. G. and Goddard, M. T. (1979). The little bronze cuckoo in New South Wales. *Australian Birds* **14**, 23–24.
- Mclean, I. G. and Maloney, R. F. (1998). Brood parasitism: recognition, and response: the options. In: *Parasitic Birds and their Hosts*. (Rothstein, S. I. and Robinson, S. K. eds) Oxford University Press, Oxford.
- Mermoz, M. E. and Reboreda, J. C. (1994). Brood parasitism of the shiny cowbird, *Molothrus bonariensis*, on the brown-and-yellow marshbird, *Pseudoleistes virescens*. *Condor* **96**, 716–721.
- Moksnes, A., Røskaft, E., Braa, A. T., Korsnes, L., Lampe, H. L., and Pedersen, H. C. (1990). Behavioural responses of potential hosts towards artificial cuckoo eggs and dummies. *Behaviour* **166**, 64–89.
- Molnar, B. (1944). The cuckoo in the Hungarian plain. *Aquila* **51**, 100–112.
- Moreno, J. and Osorno, J. L. (2003). Avian egg colour and sexual selection: does eggshell pigmentation reflect female condition and genetic quality? *Ecology Letters* **6**, 803–806.
- Moskát, C., Avilés, J. M., Ban, M., Hargitai, R., and Zolei, A. (2008). Experimental support for the use of egg uniformity in parasite egg discrimination by cuckoo hosts. *Behavioural Ecology and Sociobiology* **62**, 1885–1890.
- Moyer, D. C. (1980). On lesser honeyguide and black-colored barbet. *Zambian Ornithological Society Newsletter* **10**, 159.
- Nelson, K. J. and Jackson, R. R. (2006). Compound mimicry and trading predators by the males of sexually dimorphic Batesian mimics. *Proceedings of the Royal Society of London B* **273**, 367–372.
- Newton, A. (1896). *A Dictionary of Birds*. Adam & Charles Black, London.
- Noble, D. G. (1995). *Coevolution and ecology of seven sympatric cuckoo species and their hosts in Namibia* (PhD thesis), University of Cambridge, Cambridge.
- Øien, I. J., Moksnes, A., and Røskaft, E. (1995). Evolution of variation in egg color and marking pattern in European passerines: adaptations in a coevolutionary arms race with the cuckoo, *Cuculus canorus*. *Behavioural Ecology* **6**, 166–174.
- Payne, R. B. (1967). Interspecific communication signals in parasitic birds. *American Naturalist* **101**, 363–375.
- Payne, R. B. (1977). The ecology of brood parasitism in birds. *Annual Review of Ecology and Systematics* **8**, 1–28.
- Peer, B. D., Ellison, K. S., and Sealy, S. G. (2002). Intermediate frequencies of egg ejection by Northern Mockingbirds (*Mimus polyglottos*) sympatric with two cowbird species. *Auk* **119**, 855–858.
- Planque, R., Britton, N. F., Franks, N. R., and Peletier, M. A. (2002). The adaptiveness of defence strategies against cuckoo parasitism. *Bulletin of Mathematical Biology* **64**, 1045–1068.
- Reed, R. A. (1968). Studies of the Diederik Cuckoo *Chrysococcyx caprius* in the Transvaal. *Ibis* **110**, 321–331.
- Reynolds, S. J., Martin, G. R., and Cassey, P. (2009). Is sexual selection blurring the functional significance of eggshell coloration hypotheses? *Animal Behaviour* **78**, 209–215.
- Rothstein, S. I. (1975). Mechanisms of avian egg-recognition: do birds know their own eggs? *Animal Behaviour* **23**, 268–278.

- Rothstein, S. I. (1982). Mechanisms of avian egg recognition: which egg parameters elicit responses by rejecter species? *Behavioural Ecology and Sociobiology* **11**, 229–239.
- Rothstein, S. I. (1992). Brood parasitism, the importance of experiments and host defences of avifaunas on different continents. *Proc. VII Pan-Afr. Orn. Congr.*, 521–535.
- Rothstein, S. I. and Robinson, S. K. (1998). *Parasitic Birds and their Hosts: Studies in Coevolution*. Oxford University Press, Oxford.
- Ruxton, G. D., Sherratt, T. N., and Speed, M. P. (2004). *Avoiding Attack: The Evolutionary Ecology of Crypsis, Warning Signals and Mimicry*. Oxford University Press, Oxford.
- Sato, N. J., Tokue, K., Noske, R. A., Mikami, O. K., and Ueda, K. (2010). Evicting cuckoo nestlings from the nest: a new anti-parasite behaviour. *Biology Letters* **6**, 67–69.
- Schuetz, J. G. (2005a). Low survival of parasite chicks may result from their imperfect adaptation to hosts rather than expression of defenses against parasitism. *Evolution* **59**, 2017–2024.
- Schuetz, J. G. (2005b). Reduced growth but not survival of chicks with altered gape patterns: implications for the evolution of nestling similarity in a parasitic finch. *Animal Behaviour* **70**, 839–848.
- Schulze-Hagen, K., Stokke, B. G., and Birkhead, T. R. (2009). Reproductive biology of the European Cuckoo *Cuculus canorus*: early insights, persistent errors and the acquisition of knowledge. *Journal of Ornithology* **150**, 1–16.
- Sherratt, T. N. (2002). The evolution of imperfect mimicry. *Behavioural Ecology* **13**, 821–826.
- Smith, N. G. (1968). The advantage of being parasited. *Nature* **219**, 690–694.
- Soler, M., Martinez, J. G., Soler, J. J., and Møller, A. P. (1995a). Preferential allocation of food by magpies *Pica pica* to great spotted cuckoo *Clamator glandarius* chicks. *Behavioural Ecology and Sociobiology* **37**, 7–13.
- Soler, M. and Møller, A. P. (1990). Duration of sympatry and coevolution between the great spotted cuckoo and its magpie host. *Nature* **343**, 748–750.
- Soler, J. J. and Møller, A. P. (1996). A comparative analysis of the evolution of variation in appearance of eggs of European passerines in relation to brood parasitism. *Behavioural Ecology* **7**, 89–94.
- Soler, M., Soler, J. J., Martinez, J. G., and Møller, A. P. (1995b). Chick recognition and acceptance: a weakness in magpies exploited by the parasitic great spotted cuckoo. *Behavioural Ecology and Sociobiology* **37**, 243–248.
- Sorenson, M. D., Sefc, K. M., and Payne, R. B. (2003). Speciation by host switch in brood parasitic indigobirds. *Nature* **424**, 928–931.
- Spottiswoode, C. N. and Stevens, M. (2010). Visual modeling shows that avian host parents use multiple visual cues in rejecting parasitic eggs. *Proceedings of the National Academy of Sciences USA* **107**, 8672–8676.
- Spottiswoode, C. N. and Stevens, M. (2011). How to evade a coevolving brood parasite: egg discrimination versus egg variability as host defences. *Proceedings of the Royal Society of London B* **278**, 3566–3573.
- Spottiswoode, C. N. & Stevens, M. (2012) Host-parasite arms races and rapid changes in bird egg appearance. *American Naturalist*.
- Spottiswoode, C. N., Stryjewski, K. F., Quader, S., Colebrook-Robjent, J. F.R., and Sorenson, M. D. (2011). Ancient host-specificity within a single species of brood parasitic bird. *Proceedings of the National Academy of Sciences of the USA* **108**, 17738–17742.
- Starling, M., Heinsohn, R., Cockburn, A., and Langmore, N. E. (2006). Cryptic gentes revealed in pallid cuckoos *Cuculus pallidus* using reflectance spectrophotometry. *Proceedings of the Royal Society of London B* **273**, 1929–1934.
- Stoddard, M. C. and Stevens, M. (2010). Pattern mimicry of host eggs by the common cuckoo, as seen through a bird's eye. *Proceedings of the Royal Society of London B* **277**, 1387–1393.
- Stoddard, M. C. and Stevens, M. (2011). Avian vision and the evolution of egg color mimicry in the common cuckoo. *Evolution* **65**, 2004–2013.
- Stokke, B. G., Moksnes, A. & Røskaft, E. (2002). Obligate brood parasites as selective agents for the evolution of egg appearance in passerine birds. *Evolution* **56**, 199–205.
- Swynnerton, C. F. M. (1918). Rejections by birds of eggs unlike their own: with remarks on some of the cuckoo problems. *Ibis* **6**, 127–154.
- Takasu, F. (2003). Co-evolutionary dynamics of egg appearance in avian brood parasitism. *Evolutionary Ecology Research* **5**, 345–362.
- Takasu, F. (2005). A theoretical consideration on co-evolutionary interactions between avian brood parasites and their hosts. *Ornithological Science* **4**, 65–7.
- Tanaka, K. D. and Ueda, K. (2005). Horsfield's hawk-cuckoo nestlings simulate multiple gapes for begging. *Science* **308**, 653–653.
- Tarboton, W. (1986). African cuckoo: the agony and ecstasy of being a parasite. *Bokmakierie* **38**, 109–111.
- Tokue, K. and Ueda K. (2010). Mangrove gerygones reject and eject little bronze-cuckoo hatchlings from parasitized nests. *Ibis* **152**, 835–839.
- Van Valen, L. (1973). A new evolutionary law. *Evolutionary Theory* **1**, 1–30.

- Vernon, C. J. (1987). On the Eastern Green-backed Honeyguide. *Honeyguide* **33**, 6–12.
- Victoria, J. K. (1972). Clutch characteristics and egg discriminative ability of the African village weaverbird *Ploceus cucullatus*. *Ibis* **114**, 367–376.
- Vorobyev, M. and Osorio, D. (1998). Receptor noise as a determinant of colour thresholds. *Proceedings of the Royal Society of London B* **265**, 351–358.
- Wallace, A. R. (1889). *Darwinism: An Exposition of the Theory of Natural Selection With Some Of Its Applications*. Macmillan, London.
- Welbergen, J. A. and Davies, N. B. (2008). Reed warblers discriminate cuckoos from sparrowhawks with graded alarm signals that attract mates and neighbours. *Animal Behaviour* **76**, 811–822.
- Welbergen, J. A. and Davies, N. B. (2009). Strategic variation in mobbing as a front line of defense against brood parasitism. *Current Biology* **19**, 235–240.
- Welbergen, J. A. and Davies, N. B. (2011). A parasite in wolf's clothing: hawk mimicry reduces mobbing of cuckoos by hosts. *Behavioural Ecology* **22**, 574–579.
- Weller, M. W. (1968). The breeding biology of the parasitic black-headed duck. *Living Bird* **7**, 169–208.
- Wyllie, I. (1981). *The Cuckoo*. Batsford, London.
- Yang, C., Liang, W., Cai, Y., Shi, S., Takasu, F., Møller, A. P., Antonov, A., Fossøy, F., Moksnes, A., Røskaft, E., and Stokke, B. G. (2010). Coevolution in action: disruptive selection on egg colour in an avian brood parasite and its host. *PLoS One* **5**, e10816.

---

# Afterword

Scott V. Edwards

---

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, and 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. 110). 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. 2011). For example, in the classic 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. 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 coevolution hypothesized by Langmore and Spottiswoode to occur in many avian brood parasite systems have arisen very rapidly and recently, and may not per-

sist 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 gentes was shown to exhibit mild but significant differentiation at autosomal microsatellites (Fossey 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 coevolves 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 Edwards, S. V. (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., Antonov, A., Moksnes, A., Roskaft, E., Vikan, J. R., Moller, A. P., Shykoff J. A., and Stokke, B. G. (2011). Genetic differentiation among sympatric cuckoo host races: males matter. *Proceedings of the Royal Society B-Biological Sciences* **278**, 1639–1645.
- Joseph, L., Wilke, T., and Alpers, D. (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., and Kilner, R. M. (2010). The coevolutionary arms race between Horsfield's Bronze-Cuckoos and Superb Fairy-wrens. *Emu* **110**, 32–38.
- Langmore, N. E., Hunt, S., and Kilner, R. M. (2003). Escalation of a coevolutionary arms race through host rejection of brood parasitic young. *Nature* **422**, 157–160.
- Langmore, N. E., Srevens, M., Heinsohn, R., Hall, M. L., Peters, A., and Kilner, R. M. (2011). Visual mimicry of host nestlings by cuckoos. *Proceedings of the Royal Society of London B* **278**, 2455–2463.
- Servedio, M. R. and Hauber, M. E. (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 Payne, R. B. (2002). Molecular genetic perspectives on avian brood parasitism. *Integrative and Comparative Biology* **42**, 388–400.
- Sucgang, R., Kuo, A., Tian, X., Salerno, W., Parikh, A., Feasley, C., Dalin, E., Tu, H., Huang, E., Barry, K., Lindquist, E., Shapiro, H., Bruce, D., Schmutz, J., Salamov, A., Fey, P., Gaudet, P., Anjard, C., Babu, M.M., Basu, S., Bushmanova, Y., van der Wel, H., Katoh-Kurasawa, M., Dinh, C., Coutinho, P., Saito, T., Elias, M., Schaap, P., Kay, R., Henrissat, B., Eichinger, L., Rivero, F., Putnam, N., West, C., Loomis, W., Chisholm, R., Shaulsky, G., Strassmann, J., Queller, D., Kuspa, A., and Grigoriev, I. 2011. Comparative genomics of the social amoebae *Dictyostelium discoideum* and *Dictyostelium purpureum*. *Genome Biology* **12**:R20.
- Welbergen, J. A. and Davies N. B. (2011). A parasite in wolf's clothing: hawk mimicry reduces mobbing of cuckoos by hosts. *Behavioral Ecology* **22**, 574–579.
- Yuan, Q.-Y. and Lu, L.-Z. (2007). Progresses in inheritance of genes for avian eggshell color. *Yichuan* **29**, 265–268.