Cuckoo adaptations: trickery and tuning

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Abstract
I suggest that the cuckoo’s parasitic adaptations are of two kinds: ‘trickery’, which is how adult cuckoos and cuckoo eggs and chicks evade host defences, and involves adaptations that have co-evolved with host counter-adaptations, and ‘tuning’, which is how, once accepted, cuckoo egg and chick development are then attuned to host incubation and provisioning strategies, and which might not always provoke co-evolution. Cuckoo trickery involves adaptations to counter successive lines of host defence and includes: tricks for gaining access to host nests, egg trickery and chick trickery. In some cases, particular stages of host defences, and hence their corresponding cuckoo tricks, are absent. I discuss three hypotheses for this curious mixture of exquisite adaptation and apparent lack of adaptation: different defences best for different hosts, strategy blocking and time for evolution of defence portfolios. Cuckoo tuning includes adaptations involving: host choice and monitoring of host nests, efficient incubation of the cuckoo egg, efficient provisioning and protection of the cuckoo chick, and adaptations to avoid misimprinting on the wrong species. The twin hurdles of effective trickery in the face of evolving host defences and difficulties of tuning into another species’ life history may together explain why obligate brood parasitism is relatively rare.

Introduction
The sight of a little warbler feeding a young cuckoo, 10 times the warbler’s own body mass, has been a source of wonder to human observers for thousands of years (Schulze-Hagen, Stokke & Birkhead, 2009). Aristotle (384–322 BC), writing some 2300 years ago, knew that the common cuckoo Cuculus canorus was a brood parasite: ‘it lays its eggs in the nest of smaller birds’ (Peck, 1970). He also knew that the young cuckoo ejected the host’s eggs and young from the nest: ‘when the young bird is born it casts out of the nest those with whom it has so far lived’ (Hett, 1936). In his Natural History of Selborne (1789), Gilbert White regarded cuckoos as unnatural and ‘a monstrous outrage on maternal affection’. While Darwin (1859) was the first to explain how the cuckoo’s parasitic behaviour could have evolved by natural selection, even he referred to the young cuckoo’s ejection instinct as ‘strange and odious’.

In this review, I suggest that the cuckoo’s parasitic adaptations are of two kinds. The first, ‘trickery’, has been well studied (Rothstein & Robinson, 1998; Davies, 2000; Krüger, 2007; Kilner & Langmore, 2011). This involves the various means, by which the cuckoo evades successive lines of host defences in order to lay its eggs and to deceive the hosts into treating the cuckoo egg and chick as one of their own. These cuckoo tricks have co-evolved with host defences. However, success in trickery is only half the story.

Once the cuckoo egg and chick have been accepted, another suite of adaptations is needed to ensure that their development is attuned to the host’s incubation and provisioning strategies, which have evolved, of course, to optimize host life histories. This second type of adaptation, ‘tuning’, deserves more study.

I suggest that the twin hurdles, effective trickery in the face of evolving host defences, and difficulties of tuning into another species’ life history, may together help to explain why obligate brood parasitism, though widespread across the avian phylogeny, is a relatively rare strategy in birds, occurring in just 1% of the c. 10 000 bird species worldwide. These obligate parasites comprise: 57 species of cuckoos (Cuculidae), five species of cowbirds (Icteridae), 17 species of honeyguides (Indicatoridae), 20 species of African finches (Viduidae) and one duck (Anatidae), the black headed duck Heteronetta atricapilla from South America (Davies, 2000). Here, I focus on the parasitic cuckoos to discuss parasitic adaptations in trickery and tuning.

The evolution of cuckoo parasitism
Currently, 141 species of cuckoos (Cuculidae) are recognized and the majority (60%) are parental species, which build their own nests and raise their own young (Payne, 2005). A molecular phylogeny shows that obligate brood
parasitism has evolved independently three times within the cuckoo family from parental ancestors (Sorenson & Payne, 2005). In most of the parasitic species, just like the common cuckoo, the female lays one egg per host nest.

(i) New World cuckoos. The three species of parasitic ground cuckoos from Central and South America parasitize small passerine hosts with open or domed nests. The young striped cuckoo Tapera naevia nesting has sharp bill hooks, with which it slashes the host chicks to death (Morton & Farabaugh, 1979). These are then removed by the host parents, so the cuckoo chick is raised alone. The two Dromococcyx species have not been well studied but there are reports of host young disappearing soon after the cuckoo chick hatches, so these nestling cuckoos may also kill the host young (Payne, 2005).

(ii) Old World crested cuckoos. The four species of Clamator cuckoos parasitize medium-sized to large passerines, including bulbuls, babbblers, starlings, magpies and crows. The cuckoo chick does not kill or eject the host eggs/young and so it is often raised alongside host chicks (Payne, 2005). Even so, the cuckoo often outcompetes the host young for food, with the result that some are crushed or starve to death (Redondo, 1993; Soler et al., 1995b). In these species, a female cuckoo sometimes lays more than one egg (usually just two) in the same host nest (Soler, 1990; Martinez et al., 1998).

(iii) Old World cuckoos of the subfamily Cucudinae. This is the largest group, comprising 50 species in eleven genera. Most hosts are smaller than the cuckoo itself, usually insectivorous species of moderate size (e.g. babblers and shrikes) or of small size (e.g. warblers, chats, pipits, weavers, sunbirds). In almost all of these cuckoos, the young cuckoo ejects the host eggs or host young by balancing them on its back, one by one, and heaving them out of the nest. However, nestlings of the Asian koel Eudynamys scolopacea do not eject, nor do those of the channel-billed cuckoo Scythrops novaehollandiae (Payne, 2005). Both these cuckoos parasitize hosts of a similar size to themselves (e.g. crows), so ejection may either be too difficult, or the cuckoo may do better if it is raised alongside some host young.

**Trickery: successive stages**

It is clearly costly for a host to raise a cuckoo chick because the cuckoo either entirely destroys, or at least severely reduces, the host’s own reproductive success. In theory, therefore, hosts should evolve defences to thwart the cuckoo. These should select for cuckoo trickery, leading to selection for improved host defences, further cuckoo trickery, and so on, a cycle of co-evolution where each party evolves in response to selection pressure from the other party (Dawkins & Krebs, 1979).

There are, indeed some remarkable examples of cuckoo trickery, evolved to beat host defences, for example host-egg mimicry (Fig. 1a), but equally there are surprising examples where the hosts seem too easily fooled by cuckoo eggs and chicks unlike their own (Fig. 1b,c). This curious mixture of adaptation and lack of adaptation is an intriguing puzzle. I first review the successive lines of host defences and cuckoo trickery (Table 1), before considering why in some cases particular host defences, and hence their corresponding cuckoo tricks, are absent.

**Cuckoo tricks for access to host nests**

Female cuckoos invest a considerable time watching hosts from concealed perches (Chance, 1940). Hosts may reduce the chances that a cuckoo finds their nest by nesting further from cuckoo vantage sites (Alvarez, 1993; Øien et al., 1996; Moskát & Honza, 2000; Welbergen & Davies, 2009), by concealing their nests (Moskát & Honza, 2000; Muñoz et al., 2007), by secretive behaviour or unpredictable laying, which would make it difficult for the cuckoo to time parasitism effectively. Hosts may also reduce parasitism by...
their nest architecture, for example narrow entrance tubes to their nests, which female cuckoos find difficult to enter (Freeman, 1988; Davies, 2000).

Once a cuckoo approaches a host nest, the hosts may then mob or attack it (Moksnes et al., 1991; Roskaft et al., 2002). In reed warblers, *Acrocephalus scirpaceus*, host pairs that mobbed cuckoos strongly were less likely to be parasitized (Welbergen & Davies, 2009). Cuckoos may avoid strong mobbers because of risks of injury (more likely with larger hosts: Molnar, 1944), or because mobbing attracts predators or other brood parasites (Smith, Arcese & McLean, 1984; Krama & Krams, 2005) which increases the chance that the cuckoo herself or her egg is depredated. Mobbing also alerts neighbouring hosts (Welbergen & Davies, 2008), who then may increase their mobbing of cuckoos at their own nests (Davies & Welbergen, 2009).

Once hosts are alerted to the presence of cuckoos in their neighbourhood, they increase nest attendance and egg rejection (Davies & Brooke, 1988; Moksnes et al., 2000; Bartol et al., 2002; Davies et al., 2003). Nesting in a larger or denser colony (Brown & Lawes, 2007) or closer to neighbours (Welbergen & Davies, 2009) may reduce an individual host’s parasitism risk through corporate vigilance or dilution.

Cuckoos counter these nest defences by secretive behaviour and rapid laying (Chance, 1940). They may also benefit from hawk-like plumage, with cryptic upperparts and barred underparts, which is more prevalent in parasitic than in non-parasitic cuckoos (Payne, 1967; Krüger, Davies & Sorenson, 2007), and which disuades close approach and attack by hosts (Davies & Welbergen, 2008; Welbergen & Davies, 2011). Some cuckoo species have polymorphic female plumage, which may thwart enemy recognition by hosts (Payne, 1967; Honza et al., 2006). In great spotted cuckoos, *Clamator glandarius*, the male sometimes lures the hosts away from the nest, which allows the female to avoid host attacks while she lays (Davies, 2000). Co-operative groups of carrion crows *Corvus corone* are less likely to be parasitized by great spotted cuckoos, probably because the presence of helpers allows the incubating female to spend more time on the nest and so reduces the cuckoo’s free access (Canestrari, Marcos & Baglione, 2009).

### Cuckoo egg trickery

#### Evading host rejection

Early studies focussed on cuckoo–host interactions at the egg stage, particularly egg mimicry by cuckoos (Baker, 1913; Swynnerton, 1918). However, mimicry might be only one

### Table 1 Cuckoo trickery in response to successive lines of host defence

<table>
<thead>
<tr>
<th>Host defences</th>
<th>Cuckoo trickery</th>
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<tbody>
<tr>
<td>Nest concealment</td>
<td>Monitor hosts to find nests and time parasitism effectively</td>
</tr>
<tr>
<td>Nest further from cuckoo vantage perches</td>
<td>Secretive and rapid laying</td>
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<tr>
<td>Cryptic nests</td>
<td>Host-egg mimicry.</td>
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<tr>
<td>Decoy nests</td>
<td>Cryptic eggs</td>
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<tr>
<td>Unpredictable laying</td>
<td>Supernormal eggs</td>
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<tr>
<td>Secretive behaviour</td>
<td>Stronger egg shells</td>
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<tr>
<td>Increase surveillance and mob/attack female cuckoo</td>
<td>Destroy host clutch if reject cuckoo egg</td>
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<tr>
<td>Prevent/disuade nest inspection and laying</td>
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<tr>
<td>Nest closer to neighbours or in denser colonies</td>
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<tr>
<td>Nest architecture to reduce parasitism (e.g. narrow</td>
<td>Careful choice of nest.</td>
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<tr>
<td>entrance tube)</td>
<td>Evolve smaller size.</td>
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<tr>
<td>Desert nest or increase egg rejection if cuckoo</td>
<td>Secretive and rapid laying</td>
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<td>at nest</td>
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<tr>
<td>Reject foreign eggs</td>
<td>Host-egg mimicry.</td>
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<td>Cryptic eggs</td>
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<td>Supernormal eggs</td>
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<td>Stronger egg shells</td>
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<td>Destroy host clutch if reject cuckoo egg</td>
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<td>Egg signatures</td>
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<td>Rejection</td>
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<td>Rejection</td>
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<tr>
<td>Reject foreign chicks</td>
<td>Host-chick mimicry.</td>
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<tr>
<td>Chick signatures</td>
<td>Mimic signatures</td>
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<tr>
<td>Manipulative signals to exploit hosts</td>
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<tr>
<td>All stages</td>
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<tr>
<td>Select defences in relation to parasitism risk</td>
<td>Secretive behaviour to minimize direct cues to hosts</td>
</tr>
<tr>
<td>Rely on indirect as well as direct cues to parasitism</td>
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</tbody>
</table>

of three tricks that cuckoos employ to get hosts to accept their eggs.

**Egg mimicry**

The similarity between the eggs of the common cuckoo and those of its hosts was first noted in the mid 18th century (Jourdain, 1925; Schulze-Hagen et al., 2009). As has long been suspected (Newton, 1893), the common cuckoo species comprises several genetically different host-races (Marchetti, Nakamura & Gibbs, 1998; Gibbs et al., 2000; Fossøy et al., 2011). Each host-race tends to specialize on one host species and lays a distinctive egg type that matches, to varying degrees, the eggs of its particular host (Brooke & Davies, 1988).

Recent studies reveal that host rejection and cuckoo egg mimicry co-evolve. First, species of small birds with no history of cuckoo parasitism (because of an unsuitable diet or a nest inaccessible to female cuckoos) show little or no rejection of foreign eggs, in contrast to cuckoo hosts which often do reject eggs unlike their own (Davies & Brooke, 1989,a;b; Moksnes, Roskaft & Braa, 1991a; Moksnes et al., 1991b). Therefore, host egg rejection evolves in response to cuckoo parasitism. Second, the perfection of matching of cuckoo eggs to host eggs among the different races of the common cuckoo is related to the strength of host rejection; host species which show stronger discrimination against eggs unlike their own are parasitized by cuckoo host-races with better egg colour and pattern mimicry (Brooke & Davies, 1988; Stoddard & Stevens, 2010, 2011). For example, reed warblers reject eggs unlike their own and their cuckoo host-race has a mimetic egg (Fig. 1a), whereas dunnocks do not reject odd eggs and their cuckoo host-race lays a non-mimetic egg (Fig. 1b). Therefore cuckoo egg mimicry evolves in response to host egg rejection.

A question still unresolved is whether differences in host discrimination reflect equilibria, set by differences in the costs and benefits of egg rejection to different host species, or a continuing arms race, with younger hosts having poorer rejection, and hence cuckoo host-races with poorer egg mimicry (Stokke, Moksnes & Roskaft, 2005). Molecular phylogenies to age the various cuckoo host-races might help to answer this, but the picture is complicated because of multiple origins of host-races and then imperfect host fidelity (Marchetti et al., 1998; Gibbs et al., 2000; Fossøy et al., 2011).

**Egg crypsis**

Other cuckoo species may counter host rejection not by egg mimicry but by egg crypsis, laying dark eggs (Fig. 1d) which hosts might find more difficult to detect, especially in darker, domed nests (Brooker, Brooker & Brooker, 1990; Langmore et al., 2009b). An alternative selection pressure for egg crypsis is avoidance of detection by other female cuckoos, who remove an egg before laying their own (Brooker et al., 1990). Experiments are needed to test the importance of these two selection pressures. Evidence to date suggests that cuckoos are not selective when they remove an egg before laying and simply pick an egg at random (Davies & Brooke, 1988; Langmore & Kilner, 2009).

**Supernormal eggs**

In classic early ethological experiments, Baerends & Drent (1982) made model eggs that herring gulls Larus argentatus found even more attractive than their own eggs, because they had certain ‘supernormal’ features, such as larger size or finer speckling. It is possible that some cuckoos trick hosts with supernormal eggs. For example, Alvarez (1999) found that a host of the common cuckoo discriminated against some non-mimetic eggs yet others that contrasted markedly with their own were just as likely to be accepted as highly mimetic eggs. Future work should test whether some non-mimetic cuckoo eggs have features that hosts find particularly attractive.

**Egg signatures**

Hosts not only evolve egg rejection as a defence, their egg patterns evolve too, as distinctive ‘signatures’ to facilitate the detection of parasite ‘forgeries’. Comparative evidence supports this idea, which was first proposed by Swynnerton (1918). Host species exploited by common cuckoos have less variation in the appearance of eggs within a clutch, and more variation between clutches of different females, than do species with no history of cuckoo parasitism (Oien, Moksnes & Roskaft, 1995; Soler & Moller, 1996; Stokke, Moksnes & Roskaft, 2002). Both features make life more difficult for cuckoos since it might be easier for hosts to detect a foreign egg if all their own eggs look alike (Stokke et al., 1999; Moskát et al., 2008; but for counter-examples, see Kilner, 2006; Cherry, Bennett & Moskát, 2007) and distinctive markings for individual host females makes it harder for the cuckoo to evolve a convincing forgery for that host species’ eggs (Takasu, 2003; Stokke et al., 2007).

A translocation by humans also shows that these two features of host egg appearance evolve in response to cuckoo parasitism. When African village weaverbirds Ploceus cucullatus were introduced onto two islands, where they became isolated from their parasite, the diederik cuckoo Chrysococcyx caprius, both within-clutch uniformity and between-clutch variation declined over 60–100 generations, and this compromised the weaverbirds’ ability to detect foreign eggs (Lahti, 2005, 2006).

Host egg signatures are particularly spectacular in the tawny-flanked prinia Prinia subflava, a common host of the cuckoo finch Anomalospiza imberbis in sub-Saharan Africa (Spottiswoode & Stevens, 2010). The prinia’s eggs vary in four traits: colour (blue, white, red, olive), marking size, variation in markings and marking dispersion. Experiments involving placing foreign conspecific eggs into nests show that the prinias are more likely to reject eggs unlike their own and they pay attention to all four traits. Furthermore, these four egg traits vary independently, which is exactly
what would be expected if they had evolved to maximize the distinctiveness of signatures.

The cuckoo finch has evolved similar variation in its eggs. It would clearly pay individual female cuckoo finches to target those prinia clutches for whom their egg would be a good forgery. Perhaps this is simply not feasible because cuckoo finches lay eggs at random and so suffer high rejection rates as their egg is often a poor match (Spottiswoode & Stevens, 2010). This shows how effective host signatures can be as a defence and raises the question of why signatures are not similarly spectacular in all host species. Perhaps other selection pressures, such as the advantage of camouflage, constrain signature variation.

**Egg shell strength**

Some cuckoos and parasitic cowbirds have especially strong shells (Spaw & Rohwer, 1987; Brooker & Brooker, 1991) which are more difficult for hosts to puncture and reject (Antonov et al., 2008). Hosts are then faced with the more costly option of rejection by desertion. They may decide to accept if cuckoo eggs are difficult to distinguish with certainty (Antonov et al., 2009) or if acceptance is not too costly, because the cuckoo egg is often laid too late, or some host young can be raised alongside a cuckoo chick (Krüger, 2011). Host-races of the common cuckoo that encounter stronger rejection from their host species have thicker shelled eggs than those parasitizing less discriminating host species, as expected if egg strengthening has evolved to discourage host rejection (Spottiswoode, 2010).

**Mafia enforcement**

Finally, some brood parasites may disuade host rejection by Mafia-like enforcement, punishing hosts who reject the cuckoo egg or chick (Zahavi, 1979). There is experimental evidence for this in great spotted cuckoos (Soler et al., 1995c) and brown-headed cowbirds Molothrus ater (Hoover & Robinson, 2007). In both cases, their hosts raise some of their own young from parasitized nests so it might pay hosts to accept the cost of raising a parasitic chick, to enjoy the benefit of some personal reproductive success, rather than suffer the greater net cost of clutch destruction. However, cuckoos which kill all the host young are unlikely to be able to enforce acceptance as these hosts gain nothing from a parasitized nest.

**Cuckoo chick trickery**

Early studies puzzled over why hosts of the common cuckoo were so discriminating against eggs unlike their own, yet readily accepted the cuckoo chick, which was larger and had a different gape colour compared with their own chicks, two cues (size and colour) readily used in egg discrimination (Davies & Brooke, 1988).

One possible explanation is that chick discrimination is a greater cognitive challenge. At the egg stage, hosts imprint on their eggs the first time they breed and then reject eggs that differ from this learnt set (Rothstein, 1975; Lotem, Nakamura & Zahavi, 1995). If hosts are parasitized in their first attempt, they will imprint on both their own and parasite eggs, so there is a cost of misimprinting. Nevertheless, early learning brings a net benefit at the egg stage. In an elegant model, Lotem (1993) showed that in theory such a learning mechanism would not pay at the chick stage for hosts of ejector cuckoos; if their first breeding attempt was parasitized, they would imprint only on the cuckoo chick. In subsequent, unparasitized attempts, therefore, they would reject their own chicks. The greater cost of misimprinting at the chick stage means that the rule ‘accept any chick’ would do better than this imprinting rule. For hosts of non-evicting parasites too, theory suggests that learned recognition of brood parasite chicks is only likely to evolve under a relatively rare combination of conditions, namely low host chick survival in parasitized nests, high parasitism rates and large clutch sizes (Lawes & Matthews, 2003). A second challenge for chick discrimination is that, whereas eggs look the same throughout incubation, chicks change dramatically in appearance from day to day. With a brood hierarchy, where chicks are at different stages of development, spotting a stranger might be a difficult task (Davies & Brooke, 1988).

However, cognitive limitations cannot provide a universal constraint because recent studies reveal that hosts of some Australian bronze-cuckoos (Chalcites spp.) do often reject a cuckoo chick, either by abandoning it or by picking it up and tossing it out of the nest (Langmore, Hunt & Kilner, 2003; Sato et al., 2010; Tokue & Ueda, 2010). Single host chicks tend to be accepted, so rejection of cuckoo chicks is not simply a by-product of rejection of lone chicks. Superb fairy-wrens Malurus cyaneus were more likely to reject nestlings of an occasional parasitic cuckoo species, which were less like their own young in appearance, than nestlings of their regular parasite species, which tended to resemble their own young. This suggests that visual cues were involved in rejection. Furthermore, superb fairy-wrens that accepted a cuckoo nestling did not then abandon a lone fairy-wren nestling in later breeding attempts (Langmore et al., 2003). Therefore hosts avoid the misimprinting problem modelled by Lotem, perhaps by template-guided learning to focus learning towards features of their own young (Langmore et al., 2009a).

As predicted by co-evolutionary theory, in these cases where hosts reject foreign young, the nestlings of their respective cuckoo species have evolved visual mimicry of the host nestlings in nestling down and colour of the skin and gape flanges (Langmore et al., 2011).

Cuckoo nestlings sometimes also have begging calls which are structurally similar to those of the host chicks (McLean & Waas, 1987; Mundy, 1973; Payne & Payne, 1998; Langmore et al., 2008; Anderson et al., 2009b). Vocal mimicry may also combat host rejection. However, experiments are needed to test this because begging calls like those of host young may also be a case of ‘tuning’ to enhance host provisioning (Kilner, Noble & Davies, 1999; Grim, 2005; Madden & Davies, 2006). In non-ejector cuckoos, the nestling cuckoo has the opportunity to learn appropriate begging calls by listening to its host chick companions. Ejector
cuckoos are not able to do this. Nevertheless, they may be genetically predisposed to call like their host’s chicks (Langmore et al., 2008), and have the flexibility to modify their calls through experience, homing in on those calls which work best in stimulating host provisioning (Madden & Davies, 2006; Langmore et al., 2008).

### Minimizing parasitism cues

As cuckoos evolve improved trickery to combat these successive lines of host defence, this imposes increased costs on host defences. For example, nest defence becomes more costly when cuckoos mimic hawks, because the close inspection necessary to recognize the enemy entails risks to adult host survival. Likewise, when cuckoos evolve host-egg or host-chick mimicry, this introduces the costs of recognition errors when hosts decide whether to accept or reject eggs or chicks (Davies, Brooke & Kacelnik, 1996; Langmore et al., 2009a).

In response to these costs, hosts vary their defences in relation to the local threat of parasitism, increasing nest defence, egg rejection and chick rejection in places and at times when parasitism is more likely (e.g. nest defence: Lindholm & Thomas, 2000; Røskaft et al., 2002; Welbergen & Davies, 2009; egg rejection: Brooke, Davies & Noble, 1998; Stokke et al., 2008; chick rejection: Langmore et al., 2009a). This, in turn, selects for increased secrecy on the part of the cuckoo, to minimize direct cues to parasitism.

Hosts may then respond to such increased cuckoo secrecy in two ways. First, they may attend to their neighbours’ alarm responses, which increases the chance that they will be alerted to cuckoo activity in their local area (neighbourhood watch), and may also lead to improvements in their abilities to discriminate cuckoos from other enemies through social learning (Davies & Welbergen, 2009). Second, hosts may rely more on indirect cues to parasitism, which are impossible for cuckoos to conceal (Holen & Johnstone, 2006), for example distance to look-out perches, essential for cuckoos when searching for host nests (see references above).

### Trickery: adaptation and lack of adaptation

The various cuckoo tricks described above make good sense as responses to successive lines of host defence (Table 1). But why are particular host defences, and hence their corresponding cuckoo tricks, sometimes absent? For example, European hosts of the common cuckoo regularly reject cuckoo eggs but usually accept cuckoo chicks (Davies & Brooke, 1989b), whereas many Australian hosts do the reverse, accepting cuckoo eggs yet rejecting cuckoo chicks (Langmore & Kilner, 2010). I consider three hypotheses. They may all apply together, in concert.

### Different defences best for different hosts

In theory, early defences will bring greatest benefits. If a host can prevent parasitism through nest defence, it saves its entire clutch. If it delays defence until the egg stage, it will have lost some of its clutch because the cuckoo usually removes one or more host eggs before it lays (Davies & Brooke, 1988) or it may puncture host eggs (Soler, Soler & Martinez, 1997; see also Massoni & Reboreda, 1999; Spottiswoode & Colebrook-Robjent, 2007). If the host delays further, until the chick stage, it will have probably lost its entire clutch (ejector cuckoos) or at least some of its clutch or brood (non-ejector cuckoos). Even so, late rejection of single cuckoo chicks could still allow a replacement clutch or save resources for the next season.

### Time for evolution of defence portfolios

If some lines of host defence evolve first, and are then effectively countered by the cuckoo, older cuckoo–host
interactions will have had time for more sophisticated co-evolved adaptations, perhaps with more lines, or later lines, of defence and offence.

As an example of how ‘portfolios’ of defence (Britton et al., 2007) might evolve, imagine a newly parasitized host that attacks a cuckoo who approaches its nest, not as a specific response to the threat of parasitism, but as part of its general defence against intruders or predators. As a result of the encounter, the host might have increased motivation to inspect its nest and reject anything unusual. For example, reed warblers increase their rejection of foreign eggs even after the experience of a predatory jackdaw Corvus monedula at their nest. This rejection could then be refined as a specific response to cuckoos, whose appearance would more likely be followed by an odd egg in the nest. Thus, reed warblers are more likely to reject an egg after they see a cuckoo rather than a jackdaw at their nest (Davies & Brooke, 1988).

This initial egg rejection could be adaptive even if the hosts could not identify the cuckoo’s egg. Svenningsen & Holen (2010) show that if the hosts are certain they have been parasitized, then in theory it pays them simply to reject an egg at random. This crude behaviour would then expose the hosts to selection for egg discrimination and egg signatures. The key point is that each change in host behaviour creates a new arena of selection pressures, so behavioural change drives the potential for genetic change (Laland, Odling-Smee & Feldman, 1999). Thus defence portfolios could evolve through ‘strategy facilitation’ (Kllner & Langmore, 2011), a counter-process to that of ‘strategy blocking’.

### Tuning into host life histories

Once the cuckoo has by-passed host defences, it then has to ensure that its egg and chick development are suited to the host’s life history (Table 2).

<table>
<thead>
<tr>
<th>Host characteristics</th>
<th>Cuckoo tuning</th>
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<tbody>
<tr>
<td>Size, diet and nest</td>
<td>Choose hosts of appropriate size, diet and nest for raising young cuckoo</td>
</tr>
<tr>
<td>Laying</td>
<td>Parasitize nest during host laying period</td>
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<td></td>
<td>Depredate host clutches where incubation has begun to force hosts to lay replacement clutch</td>
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<td></td>
<td>Cognitive ability to remember the spatial and temporal availability of suitable host nests</td>
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<tr>
<td>Incubation</td>
<td>Match host incubation period by: small egg, internal incubation to give cuckoo chick a head start, pecking host eggs to arrest their development</td>
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<td></td>
<td>Host egg removal to ensure host incubation capacity is not exceeded</td>
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<tr>
<td>Chick provisioning</td>
<td>Either: (1) eject host eggs/chicks to claim all the food; (2) tolerate host chicks to increase provisioning to the brood, with increased begging to claim unfair share</td>
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<td></td>
<td>Begging display attuned to host provisioning strategies, or to exploit them</td>
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<tr>
<td>Alarm calls to warn nestlings of predators</td>
<td>Tune into host parent alarms</td>
</tr>
<tr>
<td>Imprint on host parents or brood mates to guide species recognition or future mate choice</td>
<td>Avoid imprinting for species recognition (use innate password)</td>
</tr>
<tr>
<td></td>
<td>Imprint on hosts for future host choice</td>
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</table>

### Host choice

This first involves choosing hosts of a suitable size, diet and nest type. Some hosts may have an unsuitable diet for raising a cuckoo chick, or they may have nestlings that are too large for non-ejector cuckoo chicks to compete with, or nests that are too deep for ejector cuckoos to successfully eject the host eggs (Grim et al., 2011). Then, there are suites of adaptations to ensure that the cuckoo egg and cuckoo chick are attuned to the host’s caring strategies.

### Egg tuning

One suite of adaptations ensures that the cuckoo egg is incubated efficiently and, ideally, hatches before the host’s eggs. This makes life easier for ejector cuckoo chicks (host eggs are probably easier to eject than host chicks) and also gives non-ejector cuckoo chicks a head-start in development, so they are better able to outcompete the host chicks.

Time of laying is, to some extent, selected by host defences and so is part of cuckoo trickery. Thus, cuckoo eggs laid before the hosts have begun their clutch are more likely to be rejected; very sensibly the hosts seem to follow the rule ‘any eggs appearing before I begin to lay cannot be mine!’ (Davies & Brooke, 1988; Langmore et al., 2003). Nevertheless, timing is further refined by the need for tuning. Eggs laid after the hosts have completed their clutch are readily accepted but may not receive sufficient incubation. Various cuckoo adaptations ensure that the cuckoo egg hatches in good time.

In common cuckoos, this suite of tuning adaptations (Table 2) involves the female cuckoo timing her parasitism to coincide with the host-laying period (Chance, 1940; Davies & Brooke, 1988). She also depredates host clutches too late to parasitize (where incubation has already begun), which then makes the host’s replacement clutch available for parasitism (Gártner, 1981; Gehringer, 1979). It would be interesting to know whether female cuckoos identify these
advanced clutches by pecking eggs to test their stage of development (as cowbirds do, Massoni & Reboreda, 1999), or whether they use cues from host behaviour (e.g. incubation). Female great spotted cuckoos may peck host eggs to arrest their development and ensure the cuckoo egg hatches first (Soler et al., 1997). Greater honeyguides puncture host eggs more when laying late relative to the host clutch, which also increases the chance that the parasite chick hatches (Spottiswoode & Colebrook-Robjent, 2007).

The small egg size of parasitic cuckoos, compared with those of non-parasitic cuckoos, may also ensure the cuckoo egg hatches in good time, as smaller eggs require less incubation. Egg size, too, may partly be selected by host defences, as hosts reject eggs that are much larger than their own (Davies & Brooke, 1988; Langmore et al., 2003). Nevertheless, egg size may then be further refined to facilitate hatching because the egg is laid with the strength to eject host eggs (Krüger & Davies, 2004).

Some parasitic cuckoos lay at 48 h intervals. This may not be a specific adaptation for brood parasitism, as non-parasitic cuckoos also lay at this interval. Nevertheless, this gives the potential for the parasite egg to be incubated internally inside the female’s oviduct for an additional 24 h and so facilitates early hatching because the egg is laid with embryo development already well underway. This ‘head start’ in development has been shown for the common cuckoo and the African cuckoo Cuculus gularis, and it also occurs in greater honeyguides Indicator indicator, which also lay at 48 h intervals (Birkhead et al., 2011).

A second problem concerning incubation tuning is that the addition of a parasitic egg to the host clutch may exceed the host’s incubation capacity. Female common cuckoos, and other cuckoo species, usually remove one or two host eggs before they lay. Egg removal does not increase host acceptance of a parasitic egg (and is therefore not part of trickery to deceive hosts) but is likely to improve its incubation efficiency (Davies & Brooke, 1988).

Finally, parasitic cuckoos are likely to need special cognitive skills to enable them to remember the spatial and temporal availability of suitable host nests (Clayton et al., 2001). Female parasitic cowbirds (Molothrus spp.) have a larger hippocampus than males, suggesting an adaptation to enhance spatial memory (Sherry et al., 1993; Reboreda, Clayton & Kacelnik, 1996). It is not known whether female cuckoos have similar brain specializations, though on average brood parasitic cuckoos have smaller brains in relation to their body mass compared with non-parasitic cuckoos (Payne, 2005; Boerner & Krüger, 2008).

**Chick tuning**

A further suite of adaptations enhance the development of the cuckoo chick (Table 2). In ejector species, the cuckoo is raised alone and so it gains all the food the hosts bring to the nest. Its problem is simply to ensure the hosts bring enough food. Non-ejector cuckoos, on the other hand, have the assistance of host chicks in soliciting food, but then have to compete for the food once it is delivered. These alternative strategies present different tuning problems and highlight the two functions of begging signals, namely first to stimulate the delivery of food to the brood, and then to compete for the food once it has arrived (Kilner et al., 1999).

Ejector cuckoos incur an energetic cost of ejection itself. This includes the energy expended in evicting the host eggs or young, and the time lost from soliciting food from the host parents while evicting (Anderson et al., 2009a; Grim et al., 2009). Once the cuckoo has eliminated competition from the host young, it then has to work alone to stimulate the host parents to bring it sufficient food. This involves extravagant begging signals to increase host provisioning, including rapid begging calls (Davies, Kilner & Noble, 1998; Kilner et al., 1999), colourful gapes (Alvarez, 2004) or wing patches to simulate extra gapes in the nest (Tanaka, Morimoto & Ueda, 2005; Tanaka & Ueda, 2005). Despite these costs, ejector cuckoos grow better when they are raised alone compared with when they are experimentally arranged to share the nest with host young (Hauber & Moskát, 2008; Grim et al., 2009).

Non-ejector cuckoos may tolerate host young either because host egg ejection is too costly (large host eggs or deep/large host nests makes ejection difficult: Grim et al., 2009), or because the cuckoo gains a net benefit from the presence of host young because their begging displays stimulate increased provisioning by the host parents (Kilner, Madden & Hauber, 2004). The cuckoo chick then takes an unfair share of this extra food by stretching up higher, begging first and by more elaborate begging, which manipulates the hosts into favouring it over their own young (Redondo, 1993; Soler et al., 1995b). Experiments have shown that brown-headed cowbirds (a non-ejector) increase their growth rate by tolerating some host young when raised by eastern phoebes (Kilner et al., 2004). Experiments are needed to test whether non-ejector cuckoos likewise profit by tolerating host young. Comparative studies would identify the host and parasite life-history variables that favour ejection versus non-ejection by parasites.

In both ejector and non-ejector cuckoos, therefore, the parasite chick usually begs more intensively than the host chicks. It may be costly for the hosts to resist these super stimuli because of the costs of ignoring signals from their own young, which are likely to improve the host’s success in unparasitized nests. For example, within their own broods, the most intensive begging is likely to come from their most needy chicks and their larger, fast-growing young are the ones most likely to survive (Wright & Leonard, 2002). A large, strongly begging parasite chick might therefore be irresistible to the host parents.

Common cuckoos have a longer nestling period (17–20 days) compared with the young of their host species (11–14 days). In a population of reed warblers in the Czech Republic, 16% of parasitized pairs deserted cuckoo nestlings when they were about 15 days of age (Grim, Kleven & Mikulica, 2003). Reed warblers also deserted 22% of reed warbler broods which were experimentally prolonged to exceed their normal 11–12day nestling period (by cross-fostering younger chicks; Grim, 2007). This suggests that
some host pairs reject common cuckoo nestlings not because they recognize them as foreign, but because the cuckoo demands more care than they expect to give to a normal brood of their own (Grim et al., 2003). This would select for limits to a cuckoo chick’s demands (better tuning to host provisioning capacity), or manipulative begging to persuade the hosts that extra investment was worthwhile (Redondo, 1993), or careful choice by the female cuckoo of high-quality host pairs, who might be able to provide more care (Soler et al., 1995a).

Finally, cuckoo nestlings may tune not only into host provisioning strategies but also into the alarm calls that host parents give to silence their own young when a predator approaches their nest (Davies et al., 2006). Such alarm-tuning may be particularly advantageous to cuckoos because their exuberant begging displays and prolonged nesting period are likely to increase their vulnerability to predators.

Species recognition

We now come to a potential problem of ‘mis-tuning’. How does a cuckoo know it is a cuckoo? Most species of birds do not recognize conspecifics from birth but instead learn their species characteristics during early association with their parents and siblings. In theory, brood parasites could avoid misimprinting by delayed social learning and the use of a species-specific password-like cue to focus their learning on conspecifics rather than their hosts. Such a password has been discovered in brown-headed cowbirds, who use a ‘chatter’ call to associate with other cowbirds after fledging, and then presumably learn more about their own species (Hauber, Russo & Sherman, 2001). Brown-headed cowbirds also use cues from their own plumage to form their recognition template for seeking out conspecifics (Hauber, Sherman & Paprika, 2000). Experiments are needed to test whether cuckoos, too, use passwords and self-referent phenotype matching to avoid errors in species recognition.

Nevertheless, brood parasites do imprint on their hosts as a guide to future host choice. This has been shown in the parasitic Vidua finches of Africa (Payne et al., 2000) but it is still unclear whether host choice by cuckoos develops through imprinting on hosts or on their nest or habitat characteristics (Teuschl, Taborsky & Taborsky, 1998). So far, the difficulties of breeding cuckoos in captivity has proved a barrier to experimental studies.

Trickery versus tuning

The distinction between trickery and tuning is often clear; egg mimicry is trickery (non-mimetic eggs are rejected) while internal incubation is tuning (it influences the time of hatching, not acceptance). However, in other cases the distinction is subtle. Hosts of bronze-cuckoo reject chicks unlike their own, so mimicry of host young is trickery, which enhances acceptance (Langmore et al., 2011). Hosts of common cuckoos do not reject chicks unlike their own, nevertheless a foreign chick may starve to death if its begging calls are not attuned to the host’s provisioning strategies (Kilner et al., 1999; Madden & Davies, 2006). In the first case, non-mimetic chicks are abandoned or thrown out of the nest. In the second case, mis-tuned chicks slowly starve to death. In both cases the foreign chick dies, nevertheless the trickery tuning distinction focuses on the different mechanisms of host rejection. In the first case, a cuckoo chick adaptation (mimicry) has co-evolved with host defences. In the second case, the cuckoo chick has evolved to match the host’s provisioning rules, perhaps with no co-evolved host response.

Trickery, therefore, clearly involves parasite adaptations that have evolved to counter host defences, leading to co-evolutionary changes in both hosts and cuckoos (Table 1). Could parasite tuning also provoke co-evolution? In theory hosts could escape parasitism by evolutionary changes in many of the life-history features in Table 2, including: diet, re-laying propensity, incubation, responses to egg removal and provisioning strategies. Comparative studies would reveal whether these potential changes have occurred (e.g. Hauber, 2003). Fundamental changes in life history seem less likely to evolve, or at least will take much longer, than new behavioural defences. Nevertheless parasite tuning could lead to evolutionary changes in hosts and hence promote the evolution of further parasite adaptations. I discuss two examples from other host–parasite interactions to illustrate this.

Brood parasitic Vidua finch nestlings mimic the intricate gape patterns of their host species’ young, with whom they are raised. Classically, this is regarded as a case of parasite mimicry evolved to avoid host rejection of foreign chicks, with host nestlings evolving more distinctive signatures to escape the parasite, and parasites evolving new forgeries. However, there is little evidence that the estrildid hosts reject chicks with mouth patterns unlike their own. An alternative view is that the host nestlings’ elaborate mouth markings have evolved through sibling rivalry to stimulate provisioning by their parents (Schuetz, 2005a,b). The Vidua parasitic nesting is then selected to tune into this communication system, but with the twist that it will be selected to exaggerate the signals compared with the host young. This is because the parasite’s demands will not be tempered by any genetic stake in the other chicks in the nest, nor by the host parents’ future reproduction. Once the parasite has exaggerated the signal, the host young will then be under selection to increase their signalling in order to compete effectively for care from their parents. This, in turn, will select for further exaggeration by the parasite. So this might be a case where the host chicks are evolving to match the parasite (Hauber & Kilner, 2007). If so, this would be an example of parasite tuning which has co-evolved with host responses.

A second example where parasite tuning might provoke host counter-responses, and hence co-evolution, is the puncturing of host eggs by the parasite. Female greater honeyguides I. indicator usually puncture host eggs when they parasitize a nest, which reduces the number of host young that the honeyguide hatchling needs to kill (with bill hooks) or outcompete. Spottiswoode & Colebrook-Robijnt
Evolutionary process Co-evolutionary arms race involving host 
Function To avoid host discrimination (recognition and/or 
Selection pressure Host defences Host life history 
Evolutionary process Co-evolutionary arms race involving host 
defences and cuckoo trickery Match pre-existing host parental care strategies, evoled to optimize investment in host offspring. 
May provoke co-evolutionary change 

(2007) found that thicker and rounder host eggs were more difficult for the female honeyguide to damage. Furthermore, bee-eater *Merops* spp. and kingfisher *Halcyon* spp. hosts of honeyguides have thicker egg shells than congeneric non-host species, suggesting that host eggs have evolved stronger defences in response to parasite puncturing. This would then select for more efficient puncturing by the parasite.

In both cases, parasite tuning has provoked evolutionary change in the host which, in turn, should select for changes in parasite tuning. Therefore, the trickery-tuning distinction becomes less clear when tuning provokes an evolved response in the hosts. If hosts, for example, evolve changes in their parental strategies to avoid overexploitation by parasite chicks, then mis-tuning in the parasites might be the cue that hosts use for discrimination. In this case, appropriate tuning may be how the parasitic chick avoids detection and so it becomes part of parasite trickery. Nevertheless, the distinction is clear in terms of the different selection pressures and their functions in exploiting hosts (Table 3) and may encourage more studies of the problems parasites still face, once they have succeeded in tricking the hosts into accepting the parasite’s eggs and chicks.

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### References


