Chinese Birds 2013, 4(1):86–92
DOI 10.5122/cbirds.2013.0007

SHORT COMMUNICATION

Australian cuckoos and their adaptations for brood parasitism

Naomi E. LANGMORE ✉

Evolution, Ecology and Genetics, Research School of Biology, Australian National University, Canberra, ACT, 0200, Australia

Abstract The strategies used by parasitic cuckoos to fool their hosts have intrigued naturalists and ornithologists for centuries. Here I review some of the tricks used by Australian parasitic cuckoos to increase host nest availability, access host nests, and fool their hosts into accepting their eggs and chicks. Some of these strategies are widely used by cuckoo species around the world, but other traits, such as cryptic eggs and mimetic chicks, appear to be largely restricted to the Australasian cuckoos. Generalist cuckoos face greater challenges than specialists if they must fool multiple host species, and this provides a possible explanation for why different species of cuckoos have evolved different strategies for host deception.

Keywords brood parasitism, coevolution, crypsis, cuckoo, mimicry

Introduction

Australia is home to one of the most diverse groups of parasitic cuckoos in the world, ranging from one of the world's smallest cuckoos, the Little Bronze-cuckoo (*Chalcites minutillus*, 17 g, Fig. 1, Brooker and Brooker, 1989) to the enormous Channel-billed Cuckoo (*Scythrops novaehollandiae*), which, at 610 g, is the world's largest parasitic cuckoo (Fig. 2, Brooker and Brooker, 1989). Overall, eleven species of cuckoo belonging to five genera occur in Australia (Table 1), although one of these, the Oriental Cuckoo (*Cuculus optatus*), does not breed in Australia and will not be discussed further.

The Australian cuckoos belong to the family Cuculinae, the Old World parasitic cuckoos. In all, there are 54 species belonging to 12 genera in the Cuculinae, distributed across Europe, Africa, Asia and Australasia (Davies, 2000). None of the five genera in Australia is endemic. The large Channel-billed Cuckoo is the only member of its genus and it occurs in Australia, New Guinea and Indonesia (Higgins, 1999). The Koels (*Eudynamys* spp.) are large cuckoos (120–360 g) that occur in Asia and Australasia. The medium-sized *Cuculus* cuckoos (52–150 g) are distributed throughout Europe, Africa, Asia and Australia. The *Cacomantis* cuckoos are smaller (22–44 g) and occur in Asia, New Guinea and Australia. The *Chalcites* cuckoos are the smallest cuckoos (17–35 g) and occur in Asia and Australasia (Davies, 2000).

Received 15 February 2013; accepted 14 March 2013

✉ Author for correspondence (Naomi E. Langmore)
E-mail: naomi.langmore@anu.edu.au

Brood parasitism

Parasitic cuckoos lay their eggs in the nests of other bird species. The female typically removes one of the host eggs and lays a single egg in the nest of the host. Thereafter, the female cuckoo abandons all interest in her offspring and the task of rearing the young cuckoo is borne entirely by the hosts (Fig. 3). In Australia, all except the Channel-billed Cuckoo (*Scythrops novaehollandiae*) are evicting species, meaning that the cuckoo chick evicts the host eggs or chicks from the nest soon after hatching (Fig. 4). Channel-billed Cuckoo chicks are reared alongside the chicks of their corvid hosts, although host young rarely survive to fledging (Higgins, 1999).

Some cuckoos are specialists and parasitize only a single host species, but the Australian cuckoos all parasitize more than one host. Brooker and Brooker (1989)

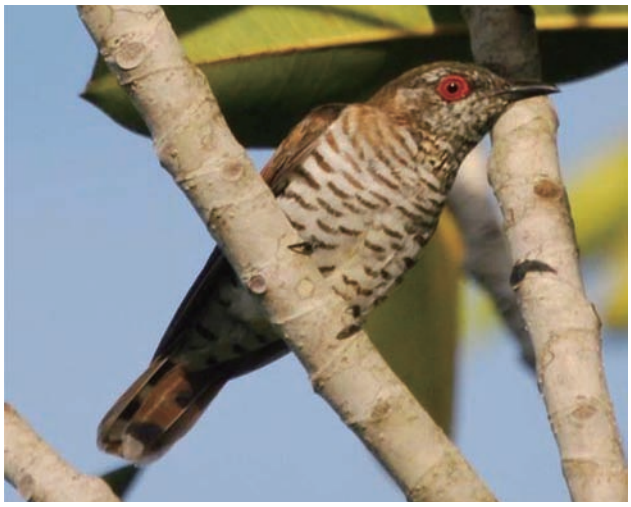

Fig. 1 A little Bronze-cuckoo (*Chalcites minutillus*), one of the world's smallest cuckoos (photo by John Grant)

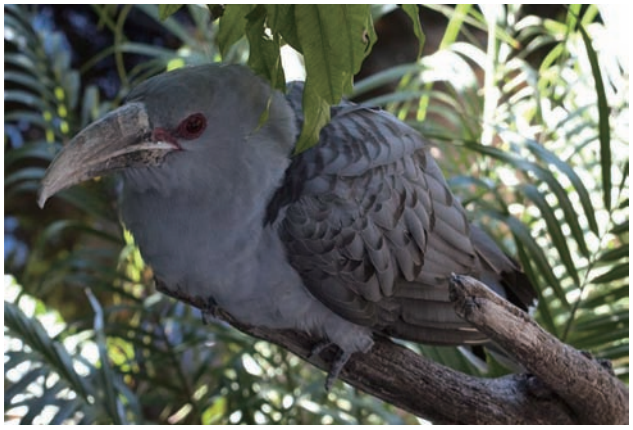

Fig. 2 A Channel-billed Cuckoo (*Scythrops novaehollandiae*), the largest parasitic cuckoo in the world (photo by Adam Jenkins)

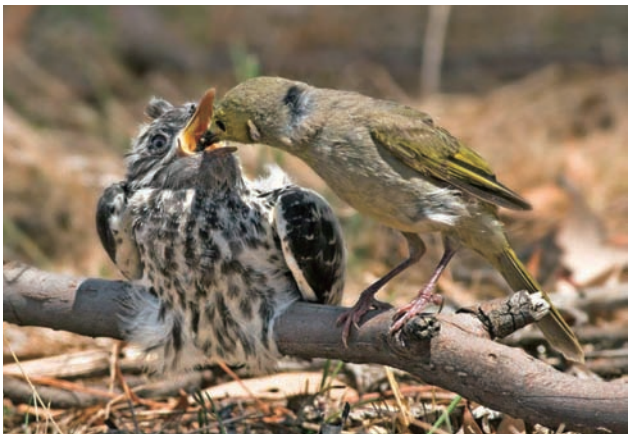

Fig. 3 A fledgling Pallid Cuckoo (*Cuculus pallidus*) receiving a feed from its foster parent, a White-plumed Honeyeater (*Lichenostomus penicillatus*) (photo by Julian Robinson)

Fig. 4 A Horsfield's Bronze-cuckoo (*Chalcites basalis*) chick shows the 'push up' posture used to evict host eggs and chicks from the nest (photo by Michelle Hall)

conducted an exhaustive survey of the hosts of Australian cuckoos and this remains the most comprehensive and detailed examination of cuckoo parasitism in Australia. The most commonly-used, successful hosts were identified as 'major hosts'. The Brookers' survey revealed that most Australian cuckoos target different major hosts (Table 1). The only exceptions were the Fan-tailed Cuckoo (*Cacomantis flabelliformis*) and the Shining Bronze-cuckoo (*Chalcites lucidus*) which shared two of the same major hosts.

Adaptations prior to egg laying

Several species of cuckoo are known to destroy the nests of hosts during late incubation or chick rearing (reviewed in Davies, 2000). This forces the host to renest, providing a ready supply of host nests at the right stage for the cuckoo to lay in. Only the female cuckoo destroys host nests, indicating that this is a strategy to increase parasitism success, rather than a simple predation event. In Australia, this behavior has been observed in the Shining Bronze-cuckoo (Morris and Catchpole, 1978) and the Fan-tailed Cuckoo (Guppy et al., unpublished data). There is also circumstantial evidence of this behavior in Horsfield's Bronze-cuckoo, because predation rates were significantly higher in weeks when the cuckoos were laying than at other times (Brooker and Brooker, 1996).

Egg laying

Few Australian cuckoos have been observed in the act of

Table 1 Australian cuckoos and their major hosts. Sources: Brooker and Brooker (1989), Erritzøe et al. (2012), webpage: lesmikebrooker.com/hosts.htm.

Cuckoo	Major hosts
Pallid Cuckoo (*Cacomantis pallidus*)	Red Wattlebird (*Anthochaera carunculata*), Yellow-throated Miner (*Manorina flavigula*), *Lichenostomus* spp., Black-headed Honeyeater (*Melithreptus affinis*)
Fan-tailed Cuckoo (*Cacomantis flabelliformis*)	White-browed Scrubwren (*Sericornis frontalis*), Brown Thornbill (*Acanthiza pusilla*), Inland Thornbill (*Acanthiza apicalis*)
Brush Cuckoo (*Cacomantis variolosus*)	*Ramsayornis* spp., Scarlet Robin (*Petroica boodang*), Leaden Flycatcher (*Myiagra rubecula*), Grey Fantail (*Rhipidura fuligonosa*)
Chestnut-breasted Cuckoo (*Cacomantis castaneiventris*)	Large-billed Scrubwren (*Sericornis magnirostra*), Tropical Scrubwren (*Sericornis beccarii*), Lovely Fairy-wren (*Malurus amabilis*)
Black-eared Cuckoo (*Chalcites osculans*)	Redthroat (*Pyrrholaemus brunneus*), Speckled Warbler (*Chthonicola sagittata*)
Horsfield's Bronze-cuckoo (*Chalcites basalis*)	Fairy-wrens (*Malurus* spp.)
Shining Bronze-cuckoo (*Chalcites lucidus*)	Thornbills *(Acanthiza* spp.)
Little Bronze-cuckoo (*Chalcites minutillus*)	Gerygones *(Gerygone* spp.)
Pacific Koel (*Eudynamis scolopacea*)	Red Wattlebird (*Anthochaera carunculata*), *Philemon* spp., Magpie-lark (*Grallina cyanoleuca*), Figbird (*Sphecotheres viridis*)
Channel-billed Cuckoo (*Scythrops novaehollandiae*)	Pied Currawong (*Strepera graculina*), *Corvus* spp.
Oriental cuckoo (*Cuculus optatus*	Non-breeding vagrant

laying their eggs in host nests. Exceptions are Horsfield's Bronze-cuckoo (*Chalcites basalis*), the Shining Bronze-cuckoo, and the Black-eared Cuckoo (*Chalcites osculans*), all of which laid their eggs in just a few seconds (Brooker et al., 1988; Higgins, 1999). The Horsfield's Bronze-cuckoos laid after the host female had laid her own eggs and laying was very rapid, ranging from 1.5 to 5.3 s (Brooker et al., 1988). Rapid laying reduces the chances that the host will detect the cuckoo and launch defenses such as mobbing of the cuckoo (Fig. 5, Langmore et al., 2012), abandonment of the nest (Langmore et al., 2003), or abandonment of the cuckoo chick (Langmore et al., 2009a).

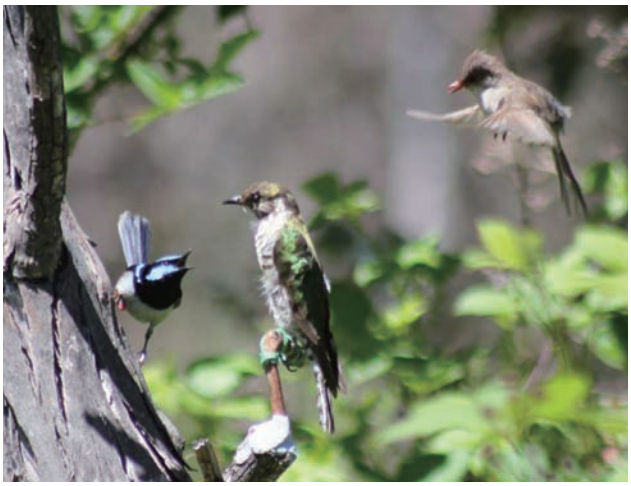

Fig. 5 Mobbing by Superb Fairy-wrens (*Malurus cyaneus*) of a Shining Bronze-cuckoo (*Chalcites lucidus*) mounted specimen (photo by William Feeney)

In the Asian Koel (*Eudynamis scolopacea*), a close relative of the Pacific Koel (*E. orientalis*) in Australia, collaboration between the male and female has been observed during egg laying (Lamba, 1966). The male flies to the host nest first, inducing the hosts to attack it, then lures them away allowing the female to access the nest and lay her egg. It is not known whether this behavior also occurs in the Pacific Koel in Australia.

Cuckoo eggs

Many cuckoos around the world have evolved egg mimicry; eggs that mimic the pattern and color of the eggs of their host (Kilner, 2006; Stoddard and Stevens, 2011). This reduces the likelihood that the cuckoo egg will be rejected by the host (Spottiswoode and Stevens, 2010). However, parasitism of more than one host species creates a problem for the cuckoo, if different hosts lay different egg types. Australian cuckoos have evolved several ingenious means of fooling their hosts through egg morphology. Some species, such as Horsfield's Bronze-cuckoo, lay a single egg type that is a good match of the eggs of both its major hosts, Fairy-wrens (*Malurus* spp.) (Fig. 6; Langmore et al., 2003; Langmore and Kilner, 2009), and its secondary hosts, thornbills (*Acanthiza* spp.). Other species have evolved polymorphic egg types, each of which resembles the egg of a different host. For example, the Brush Cuckoo (*Cacomantis variolosus)* lays three egg types, each of which matches its major host in a particular region of

its distribution (Beruldsen, 2003). Similarly, the Pallid Cuckoo (*Cacomantis pallidus*), which primarily parasitizes honeyeaters, has evolved multiple egg types, each of which is a close match of the egg of a different host (Starling et al., 2006). However, the color differences between these host-specific egg types are so subtle that they had not been detected by human observation, and the use of reflectance spectometry was needed to quantify their color and differentiate between them (Starling et al., 2006).

Rather than relying on egg mimicry, the Shining Bronze-cuckoo and Little Bronze-cuckoo have evolved an alternative disguise for their eggs. They lay dark brown or olive-green eggs that look quite unlike the eggs of their hosts (Fig. 7). The eggs are so thickly coated with dark pigment that the pigment can be wiped off a freshly laid egg. These cuckoos lay their eggs in dark, dome-shaped nests (Fig. 8) and the color and luminance of the eggs are indistinguishable to a bird's eye from those of the nest lining inside the dark nest, effectively rendering the eggs invisible to the host (Langmore et al., 2009b). Rejection of cuckoo eggs by the hosts of these cuckoos is virtually unknown (Gill, 1983; Brooker and Brooker, 1989; Langmore et al., 2005, 2009).

Although dark, dome-shaped nests constrain cuckoo egg recognition via visual cues, hosts could still use tactile cues to detect an unusually sized egg. The Superb Fairy-wren hosts of Horsfield's Bronze-cuckoo rarely reject an oddly coloured egg, but they are more likely to desert a clutch of eggs containing an egg larger than their own (Langmore et al., 2003). This has selected for a small egg relative to the cuckoo's body mass in Horsfield's Bronze-cuckoo (Krüger and Davies, 2004). Many parasitic cuckoo species have also evolved unusually strong eggshells as adaptations to parasitism, including several Australian species (Picman and Pribil, 1997).

Fig. 6 A Horsfield's Bronze-cuckoo (*Chalcites basalis*) egg (below) with two eggs of its host, a Superb Fairy-wren (*Malurus cyaneus*) (photo by Naomi Langmore)

Fig. 7 A triple-parasitized Large-billed Gerygone (*Gerygone magnirostris)* clutch from Cairns, showing the host egg (top) and three Little Bronze-cuckoo (*Chalcites minutillus*) eggs (photo by Golo Maurer)

Cuckoo chicks

The chicks of most cuckoo species, including most Australian cuckoos, look quite unlike the host chicks. There has been no selection for chick mimicry because in general hosts do not recognize and reject chicks that look different from their own. However, several hosts of the Australian Bronze-cuckoos (*Chalcites* spp.) are unusual in that they reject cuckoo chicks, rather than cuckoo eggs (Langmore et al., 2003; Sato et al., 2010; Tokue and Ueda, 2010). This may be a consequence of the poor

Fig. 8 A Little Bronze-cuckoo (*Chalcites minutillus*) chick in the dark, dome-shaped nest of its host, a Mangrove Gerygone (*Gerygone levigaster*) (photo by Naomi Langmore)

visibility inside their dark nests, which constrains detection of foreign eggs (Langmore et al., 2005, 2009b). In response to rejection by hosts, Bronze-cuckoo chicks have evolved to be striking visual and vocal mimics of the young of their major hosts (Fig. 9, Langmore et al., 2008, 2011) and non-mimetic nestlings suffer a survival cost (Langmore et al., 2003). Horsfield's Bronze-cuckoo is the most generalist of these cuckoos, and parasitizes a range of different host species (Table 1). This cuckoo faces the problem of how to mimic the young of several distinct species. It has evolved two solutions to this problem. First, to mimic the begging calls of different host young, the cuckoo produces the call of its primary host as the default call soon after hatching. However, if it is in the nest of a secondary host it rapidly modifies its begging call over several days until it becomes indistinguishable from the calls of the host young (Langmore et al., 2008). This is a particularly impressive feat given that the cuckoo chick evicts the host young before hatching and never hears their calls. It seems likely that the calls are refined through reinforcement by host parents, specifically by selective provisioning in response to more accurately mimetic calls (Langmore et al., 2008). This solves the problem of how to prevent detection of the cuckoo chick by hosts through vocal cues. However the cuckoo still faces the problem of how to mimic the appearance of host young of several different species. The hosts of Horsfield's Bronze-cuckoo produce chicks that range in skin colour from pink to grey to black. This appears to have selected for imperfect mimicry of several different host species in the cuckoo chick, which has evolved two-tone coloration. The chick has a grey head, pink upper back and grey lower back (Fig. 9, bottom panel, Langmore et al., 2011). This two-tone color-

Fig. 9 Newborn Bronze-cuckoo chicks (left) are visual mimics of their hosts (right). Top: Little Bronze-cuckoo (*Chalcites minutillus*) and Large-billed Gerygone (*Gerygone magnirostris*). Middle: Shining Bronze-cuckoo (*Chalcites lucidus*) and Yellow-rumped Thornbill (*Acanthiza chrysorrhoa*, below) and Buff-rumped Thornbill (*Acanthiza reguloides,* above). Bottom: Horsfield's Bronze-cuckoo (*Chalcites basalis*) and Superb Fairy-wren (*Malurus cyaneus*) (photos by Naomi Langmore, Golo Maurer).

ation probably allows the cuckoo to partially resemble host young, perhaps thereby reducing the probability of rejection by hosts. This cuckoo has evolved a 'jack of all trades' strategy, being an imperfect mimic of several genera rather than a specialist mimic of few closely-related species like the other Bronze-cuckoos.

Although there have been many fascinating discoveries about Australian cuckoos and the tricks they have evolved to fool their hosts, there is still much to discover. For example, how do hosts of the Little Bronze-cuckoo distinguish the cuckoo chick from their own young when mimicry of host young by the cuckoo is so accurate? Have the cryptic eggs of Bronze-cuckoos evolved to prevent rejection by hosts or by other female cuckoos that parasitize the same nest? Why do not Channel-billed Cuckoo chicks evict the host young from the nest like other Australian cuckoos? These and other questions will stimulate research for many years to come.

Acknowledgments NEL was supported by an Australian Research Council Australian Research Fellowship. I thank William Feeney, John Grant, Michelle Hall, Golo Maurer and Julian Robinson for providing photos, Wei Liang for inviting this article, and two anonymous reviewers for commenting on the manuscript.

References

Beruldsen G. 2003. Australian Birds: Their Nests and Eggs. G. Beruldsen, Kenmore Hills, Queensland.

Brooker MG, Brooker LC, Rowley I. 1988. Egg deposition by the bronze-cuckoos *Chrysococcyx basalis* and *Ch. lucidus*. Emu, 88:107–109.

Brooker MG, Brooker LC. 1989. Cuckoo hosts in Australia. Aust Zool Rev, 2:1–67.

Davies NB. 2000. Cuckoos, Cowbirds and Other Cheats. T & A D Poyser, London.

Erritzøe J, Mann CF, Brammer FP, Fuller RA. 2012. Cuckoos of the World. Christopher Helm, London.

Gill BJ. 1983. Brood parasitism by the shining cuckoo *Chrysococcyx lucidus* at Kaikoura, New Zealand. Ibis, 125:40–55.

Higgins PJE. 1999. Handbook of Australian, New Zealand and Antarctic Birds. Volume 4: Parrots to Dollarbird. Oxford University Press, Melbourne.

Kilner RM. 2006. The evolution of egg colour and patterning in birds. Biol Rev, 81:383–406.

Krüger O, Davies NB. 2004. The evolution of egg size in the brood parasitic cuckoos. Behav Ecol, 15:210–218.

Lamba BS. 1966. The egg-laying of the Koel *Eudynamys scolopacea* (Linnaeus). Bombay Nat Hist Soc, 63:750–751.

Langmore NE, Cockburn A, Russell AF, Kilner RM. 2009a. Flexible cuckoo chick rejection rules in the superb fairy-wren. Behav Ecol, 20:978–984.

Langmore NE, Feeney WE, Crowe-Riddell J, Luan H, Louwrens KM, Cockburn A. 2012. Learned recognition of brood parasitic cuckoos in the superb fairy-wren *Malurus cyaneus*. Behav Ecol, 23:798–805.

Langmore NE, Hunt S, Kilner RM. 2003. Escalation of a coevolutionary arms race through host rejection of brood parasitic young. Nature, 422:157–160.

Langmore NE, Kilner RM, Butchart SHM, Maurer G, Davies NB, Cockburn A, MacGregor NA, Peters A, Magrath MJL, Dowling DK. 2005. The evolution of egg rejection by cuckoo hosts in Australia and Europe. Behav Ecol, 16:686–692.

Langmore NE, Kilner RM. 2009. Why do Horsfield's bronze-cuckoo *Chalcites basalis* eggs mimic those of their hosts? Behav Ecol Sociobiol, 63:1127–1131.

Langmore NE, Maurer G, Adcock GJ, Kilner RM. 2008. Socially acquired host-specific mimicry and the evolution of host races in Horsfield's bronze-cuckoo *Chalcites basalis*. Evolution, 62:1689–1699.

Langmore NE, Stevens M, Maurer G, Heinsohn R, Hall ML, Peters A, Kilner RM. 2011. Visual mimicry of host nestlings by cuckoos. Proc R Soc Lond B, 278:2455–2463.

Langmore NE, Stevens M, Maurer G, Kilner RM. 2009b. Are dark cuckoo eggs cryptic in host nests? Anim Behav, 78:461–468.

Morris AK, Catchpole B. 1978. Removal of eggs by a Shining Bronze-Cuckoo. Emu, 78: 234.

Picman J, Pribil S. 1997. Is greater eggshell density an alternative mechanism by which parasitic cuckoos increase the strength of their eggs? J Ornithol, 138:531–541.

Sato NJ, Tokue K, Noske RA, Mikami OK, Ueda K. 2010. Evicting cuckoo nestlings from the nest: a new anti-parasitism behaviour. Biol Lett, 6:67–69.

Spottiswoode C, Stevens M. 2010. Visual modeling shows that avian host parents use multiple visual cues in rejecting parasitic eggs. Proc Natl Acad Sci, 107:8672–8676.

Starling M, Heinsohn R, Cockburn A, Langmore NE. 2006. Cryptic gentes revealed in pallid cuckoos *Cuculus pallidus* using reflectance spectrophotometry. Proc R Soc Lond B, 273:1929–1934.

Stoddard MC, Stevens M. 2011. Avian vision and the evolution of egg color mimicry in the common cuckoo. Evolution, 65:2004–2013.

Tokue K, Ueda K. 2010. Mangrove gerygones *Gerygone laevigaster* eject little bronze-cuckoo *Chalcites minutillus* hatchlings from parasitized nests. Ibis, 152:835–839.

澳大利亚的杜鹃及其寄生适应性

Naomi E. LANGMORE

（澳大利亚国立大学生物学研究学院）

摘要：长期以来，人们一直对寄生性繁殖的杜鹃所采用的种种计谋惊叹不已。本文对澳大利亚的寄生杜鹃如何增加寄生巢的可获得性、如何寻找和接近巢以及如何让宿主接受它们的寄生卵与雏鸟进行了综述。这些杜鹃所采用的对策，有一些是世界上其他杜鹃种类也采用的，但有一些对策，如产隐蔽的卵和模拟的雏鸟，却似乎仅见于澳大利亚的杜鹃。泛性寄生的杜鹃因为要应对较多种类的宿主，难度自然远大于专一性寄生的杜鹃种类，这同时也解释了为什么不同种类的杜鹃进化出不同的寄生策略，以避免不同宿主的识别。

关键词：巢寄生，协同进化，隐蔽，杜鹃，模拟