too: being a parent is risky and uses up a lot of energy. Parental care can be particularly costly for males. Multiple mating with males by females means that males typically have lower probability of paternity than females. As a result, males are generally expected to provide more parental care when offspring in the brood are more likely to be theirs. In other words, when males are more assured of their paternity they are more likely to provide parental care.

For burying beetles, however, the reality is slightly more complex. Experiments show that males do respond to greater paternity assurance by increasing their parental care, but only if they are young and they have a chance of breeding again: old males are better fathers and care less about female infidelity. Females provide more care than males and compensate for changes in male behaviour, increasing care when with young, insecure males and decreasing care when with old males, so reproductive success is not affected by how males respond to their assurance of paternity. As a result, the probability of parentage is not likely to be an important variable in explaining patterns of male care in burying beetles (and perhaps, other taxonomic groups too).

**So if probability of parentage is not likely to be that important what is?**

The benefits of seeking greener reproductive pastures elsewhere are likely to depend largely on how difficult it is to gain such mating opportunities. This will depend upon things like the operational sex ratio (the ratio of sexually available males to females), the availability of carcasses for breeding and the amount of competition for these carcasses. For example, if it is hard to find new females or new carcasses to breed on, males may be better off providing parental care to protect their current brood than seeking new breeding opportunities. Paradoxically, when there is high competition among males for females and breeding resources this might actually intensify sexual selection, increasing the benefits of investing in mating over parental care for highly competitive males. It is possible that the unusual complexity and flexibility of sex roles in parental care and mating strategies in burying beetles may be largely explained by inter-relationships between the unpredictability in the availability of the carcasses they need for breeding and dynamic variation in the social environments that they experience. However, these ideas need testing.

**How can these ideas be tested?**

Unlike with most vertebrates that have extended parental care, it is possible to study burying beetles in the wild and in the more controlled environment of the lab. In addition, their rapid generation times mean that it is relatively easy to apply experimental evolution in the lab, selecting on key traits of interest to see how patterns of parental care evolve. Burying beetle behaviour can also be filmed remotely in the wild and in the lab, and the availability of the resources they need to breed (small vertebrate carcasses) can be manipulated independent of the social environment they experience. This opens up exciting opportunities to understand how sex roles in parental care evolve in response to ecology (the availability of critical resources for breeding), and more generally, how parental care can facilitate adaptive, plastic responses of organisms to rapid changes in their environment.

**Where can I find out more?**


### Bird brood parasitism

**Primer**

**Bird brood parasitism**

Martin Stevens

For many animals, the effort to rear their young is considerable. In birds, this often includes building nests, incubating eggs, feeding the chicks, and protecting them from predators. Perhaps for this reason, about 1% of birds (around 100 species) save themselves the effort and cheat instead. They are obligate brood parasites, laying their eggs in the nests of other species and leaving the hosts or foster parents to rear the foreign chicks for them. Some birds also cheat on individuals of the same species (intraspecific brood parasitism). Intraspecific brood parasitism has been reported in around 200 species, but is likely to be higher, as it can often only be detected by genetic analyses.

Currently, research suggests that obligate interspecific brood parasitism arose seven times independently during evolution. This includes three origins among cuckoos, and then one origin each in cowbirds, honeyguides, estrildid finches, and a South American duck. Brood parasites are often used as model systems for investigating evolutionary arms races and coevolution in the wild. A common scenario is that, during the course of evolution, a brood parasite begins to target a new host species, with the parasitized individuals suffering costs. Then, hosts evolve an ability to recognize foreign eggs and remove them from the nest, followed by the parasite evolving mimicry of host eggs to evade detection, hosts with improved rejection abilities, and so on. Note, however, that this simplistic scenario does not neatly fit many species that have been studied. Furthermore, what we observe in many systems seems to reflect different evolutionary stages that hosts and parasites are at, as well as entirely different trajectories of coevolution.

Until recently, much of what we knew about brood parasites was based primarily on a relatively small...
number of species, in particular some cowbirds and the common cuckoo (*Cuculus canorus*). These have proven extremely productive and informative systems to understand the natural history of brood parasites, how they deceive their hosts, and how hosts can fight back to protect themselves and their offspring. However, recently, researchers have studied many other brood parasites, extending our understanding of the diversity of host–parasite interactions, and sometimes counteracting previous ideas.

**The common cuckoo — a model brood parasite?**

The most widely studied brood parasite in Europe is the common cuckoo. It is an inter-continental migrant, spending much of the year in Africa and breeding in a wide range of European countries in the spring and early summer. Although their calls are an iconic symbol of spring and summer, cuckoos are typically elusive birds and not frequently seen. Like many parasites, they no doubt gain an advantage by being hidden from their hosts; indeed, hosts are more likely to reject foreign eggs if they have recently seen a cuckoo. Apart from their reproductive behaviour, little is known about other aspects of the cuckoo’s life. In the UK, common cuckoos are in serious decline. Correspondingly, a recent study shows that in some locations a common host, the reed warbler (*Acrocephalus scirpaceus*), shows weaker defences against cuckoos today than it did in the past.

Although we do not know a great deal about their non-breeding behaviour, we know much more about the parasitic adaptations of common cuckoos, including their ways of tricking hosts, and how the foster parents fight back. If all goes to plan for a female cuckoo, she watches a potential host nest from a distance (often from a nearby tree) until the host has started laying eggs. Then, she swoops down when the nest is vacant, removes a host egg, and replaces it with one of her own. Once this is accomplished, she plays no further part in the chick’s rearing, and instead looks for other nests to target. The cuckoo chick often hatches in advance of the host’s own young, and while naked and blind heaves the foster parents’ eggs (or chicks) from the nest. By doing so, it can monopolise the parental care. The cuckoo chick grows rapidly, and in many cases reaches a size or mass considerably greater than an adult host parent by the time it fledges. This story is played out in many different host species because different female cuckoos correspond to different lineages or ‘host races’; each female cuckoo primarily specialises on targeting a given host species. For example, some females parasitize dunnocks, whereas others target bramblings or robins. This female specialisation enables each lineage to develop adaptations towards their preferred host.

Clearly, being parasitized poses a cost to hosts. Not only do they fail to rear any of their own offspring, but they also have to expend great time and energy feeding a chick to which they bear no relation. Consequently, common cuckoo hosts have evolved a suite of defences against cuckoos. First, many hosts mob a cuckoo near the nest and emit alarm calls when doing so, with the aim of driving away the cuckoo. Neighbouring pairs that observe this are also more likely to subsequently mob cuckoos. Second, hosts often eject foreign eggs from the nest. With a few exceptions, most work on brood parasite hosts shows that they primarily reject eggs not by spotting the odd egg out in the nest, but rather by learning what their own eggs look like and rejecting any egg that looks sufficiently different.

In return, cuckoos have evolved defensive counter-adaptations. They resemble a bird of prey (such as a sparrow hawk), causing hosts not to mob them and to flee instead. Often their eggs display quite a sophisticated mimicry of the colour and patterns of host eggs to prevent rejection.

The strength of these defences and counter-adaptations depends on the host species and cuckoo host race. In some species, such as the brambling, hosts have very strong rejection behaviour and cuckoos have evolved very close mimicry for both egg colour and pattern. In contrast, dunnocks are a classic example of a host species that does not reject at all, and correspondingly, cuckoos show no egg mimicry. Perhaps dunnocks are a recent host and have not had enough time to evolve defences. Other host–parasite pairs are somewhere in between.

Somewhat surprisingly, even though common cuckoo chicks look nothing like the host young, they do not seem to get rejected. An explanation appeared to be that if hosts were parasitized in their first breeding attempt, then they would learn to recognise a cuckoo chick as their own. In subsequent breedings, they would thus reject all their own young. This elegant idea was thought to apply to all brood parasites. However, as we will see below, chick rejection has now been found to take place in...
some hosts of Australian cuckoos. So, why these systems differ and whether imprinting actually occurs remains unclear.

If the common cuckoo egg gets past the host defences, the chicks possess a range of adaptations to obtain as much food as possible. They tend to use highly exaggerated begging calls and displays (including striking mouth colours). The chicks’ vocalisations often resemble the begging calls of an entire brood of the hosts’ own young. This is probably not true mimicry, however, but may be an exaggerated ‘supernormal’ stimulus that is especially effective at stimulating hosts to bring more food. Either way, play-back experiments show that the exaggerated calls are important in increasing host provisioning.

Other species of brood parasite have more elaborate means to acquire lots of food from hosts. The Japanese Horsfield’s hawk cuckoo (Cuculus fugax) has chicks with a bright yellow patch on the underside of each wing that they raise and display when host parents come to the nest (Figure 1). Painting these patches black reduces the level of provisioning by the host parents, and it seems that they work by mimicking yellow gapes and simulating the presence of multiple chicks in the nest. Many African Vidua finches show a close similarity to the gape patterns and bright mouth spots of their hosts. As with the common cuckoo begging display, this is probably not mimicry but rather convergence between the host and parasite begging signals in producing highly effective displays to stimulate hosts to provide more food (sensory exploitation).

Beyond the common cuckoo

Although the common cuckoo and its European hosts are a valuable model system, it is increasingly apparent that things can vary greatly in other species. For example, there are about 10 species of cuckoo in Australia, and as in common cuckoos, different females often target specific host species. However, one of the striking differences is that many hosts of Australian cuckoos do not reject foreign eggs. The reasons are unclear and may vary among species. For example, the dark olive brown eggs of the Gould’s bronze-cuckoo (Chalcites russatus) show little mimicry of those of the large-billed gerygone (Gerygone magnirostris), and the host shows little rejection behaviour. Research suggests that the cuckoo eggs are effectively camouflaged inside the dark nests of the hosts to prevent their eggs being detected by hosts in the first place.

Some Australian cuckoos, however, do lay eggs that are a good match to those of their main hosts (e.g. superb fairy wrens, Malurus cyaneus, by Horsfield’s bronze cuckoos, Chalcites basalis), yet the hosts also show little rejection behaviour. One suggestion is that hosts once rejected cuckoo eggs but no longer do so because the mimicry has become too good to enable reliable rejection. However, this seems unsatisfactory for several reasons, most notably because the level of mimicry is not unusually good, and not as refined as in many parasite–host groups where hosts do still reject. There is also further intrigue in these systems. Some Australian hosts reject and throw foreign chicks from the nest, or even desert nests with lone cuckoos. In some species, this has led to wonderful mimicry by the cuckoo chicks of the host young (Figure 2). Another recent study found evidence that in superb fairy wrens, mothers teach their chicks specific call components (‘passwords’) by singing to them while still in the egg.
They potentially use the calls the chicks sing back later to discriminate between their own young and cuckoo chicks. Cuckoo eggs, by contrast, are generally laid when hosts don’t sing, so their chicks cannot learn the ‘password’ calls. This mechanism could help shed light on why some Australian hosts seem to have skipped defences at the egg stage in favour of defences that operate later during offspring development. No doubt, however, more remains to be discovered, in particular why are these Australian systems so different to the common cuckoo?

The recent work in Australian cuckoo groups has enhanced our understanding of brood parasite–host interactions, and how variable they can be. This is also true of recent work on several African systems. For example, like the common cuckoo, both the diederik cuckoo (Chrysococcyx caprius) and the African cuckoo finch (Anomalospiza imberbis) parasitize host species whose eggs look rather different. However, in these species the situation is more extreme than in the common cuckoo. In particular, many host species, and the corresponding host race of the parasite, have evolved remarkably high variation in egg colour and pattern among individuals. In the most common host of the cuckoo finch, the tawny flanked prinia (Prinia subflava), individual females lay eggs varying from red to blue, to white, to olive, marked with a high diversity in patterns (Figure 3). Such variation among individuals means that different hosts have highly divergent egg colours. Because each cuckoo finch female can only lay one egg type, there is only a subset of potential host individuals whose eggs match hers well. In effect, the hosts thus reduce the number of parasites that they are susceptible to. This high variation in egg appearance is likely to have evolved under negative frequency-dependent selection, whereby new or rare egg phenotypes are at a selective advantage in the population, driving increased variation in egg colours over time. Interestingly, in cuckoo finch hosts, the degree of egg variation differs among species. Moreover, host species with low egg variation show refined rejection behaviour, whereas those with very high variation seem less discriminating. Overall, however, both strategies seem effective ways of detecting a cuckoo finch egg (one is good at detecting highly mimetic eggs, the other is good at making effective mimicry unlikely). Intrasppecific egg variation has also been shown, albeit to a smaller degree, in some Chinese hosts of the common cuckoo. This shows that the adaptations found in Chinese populations and hosts may be quite different from what we know from European common cuckoo systems.

Another African parasite that has recently been studied is the greater honeyguide (Indicator indicator). This species lacks the variation in egg colours found in many species but has some other fascinating traits. First, there has been a close convergence in egg shape and size between many honeyguide host races and their hosts; the species is separated into two ancient lineages that parasitize either ground- or tree-nesting hosts. This convergence is probably not driven by host rejection, but instead by the honeyguides themselves: for at least one host, female honeyguides puncture and destroy other conspecific eggs in a nest; thus, honeyguide eggs that look more like the host eggs might have an advantage. Second, honeyguide chicks do not evict other young from the nest, but instead they use a sharp spine on the end of their bill tip to stab the other chicks to death.

The brown-headed cowbird (Molothrus ater) is the only brood parasite that is widespread in North America. It has spread considerably and increased in numbers in recent years, and exploits more than 200 host species, with sometimes extremely high rates of parasitism. Hosts of cowbirds are often considered as either acceptors or rejectors. Rejector species, seemingly like most other brood parasite hosts, reject eggs based on whether they are different from a template of the host’s own
eggs, rather than appearing to be the odd one out in the clutch. However, brown-headed cowbirds seem not to vary much in their egg coloration and there is little evidence for egg mimicry. The cowbird chicks usually do not evict the host young from the nest but instead compete vigorously with them. In smaller host species, the young will often die of starvation, whereas in larger hosts all chicks can sometimes fledge. Unlike in the common cuckoo, which benefits from evicting the host nestlings to reduce competition, brown-headed cowbirds seem to benefit by keeping the host young in the nest because this maintains high provisioning by the parents. Because the parasitic chick is larger, it is still able to monopolise the food and to obtain a higher proportion of it than the host chicks.

The other four parasitic cowbird species are found principally in Central and South America. They vary in terms of host use, from the shiny cowbird (M. bonariensis), which utilises many host species, to the screaming cowbird (M. rufaaxillaris), which generally specialises on just one. Like the brown-headed cowbird, rates of parasitism by shiny cowbirds vary greatly and can be very high. In contrast to the brown-headed cowbird, the eggs of shiny cowbirds vary substantially in terms of colour and pattern. However, many of their hosts do not reject foreign eggs, and shiny cowbirds often do not seem to show obvious specialisation towards particular hosts. The reasons for such high egg variation are unclear. Recent work in Argentina shows that screaming cowbird fledglings have plumage colours and begging calls that are more similar to their primary hosts (baywing cowbirds, Agelaioides badius; a non-parasite) than are non-mimetic shiny cowbird young. Experiments putting either screaming or shiny cowbird young in baywing nests show high mortality of shiny cowbirds but little mortality of screaming cowbirds. This suggests that hosts reject parasitic young shortly after fledging by stopping feeding non-mimetic fledglings, which subsequently die. The conundrum here is why hosts wait until the fledgling stage to reject foreign chicks, by which time they have already invested a great deal of time and energy.

Our knowledge of the diversity brood parasites and their hosts, in particular their breeding adaptations, has substantially improved in recent years, in part through study of a greater range of species. The more we study brood parasites, the more we have to learn and to gauge the range of their adaptations we find. Exciting questions remain, including whether chick mimicry exists other systems, why such differences in evolutionary trajectories and adaptations have occurred among species, and what other deceptive traits parasites have that we have yet to discover. We know very little about the various species of brood parasite that live in under-studied parts of the world, especially areas of east and southeast Asia and New Guinea, so stay tuned for more surprises.

Further reading

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A new galloping gait in an insect

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An estimated three million insect species all walk using variations of the alternating tripod gait [1]. At any one time, these animals hold one stable triangle of legs steady while swinging the opposite triangle forward. Here, we report the discovery that three different flightless desert dung beetles use an additional gallop-like gait, which has never been described in any insect before. Like a bounding hare, the beetles propel their body forward by synchronously stepping with both middle legs and then both front legs. Surprisingly, this peculiar galloping gait delivers lower speeds than the alternating tripod gait. Why these beetles have shifted so radically away from the most widely used walking style on our planet is as yet unknown.

Like all insects described so far, four of seven observed species of Pachysoma, a dung beetle genus endemic to the coastal deserts of South Africa and Namibia, typically walk with an alternating tripod gait (Supplemental information). In this gait, the first and third leg on one side of the body move in unison with the contralateral middle leg [2] (Figure 1A,C), forming a moving tripod. This tripod alternates with the static, stable tripod made up of the remaining three legs. In many insects, this pattern of leg coordination changes with speed, creating a continuum of stepping patterns ranging from the tripod gait to a ‘tetrapod gait’, where only two legs (diagonally opposed, one on either side) swing at any one time [3–5]. All of these seemingly diverse patterns, however, follow a small set of simple rules [2], including the principal rule that each leg moves out of phase with its contralateral pair, i.e. legs of a pair move alternately. In almost all insect species, synchronous (in-phase) stepping of a leg pair is only observed in exceptional