Brood parasitism selects for no defence in a cuckoo host

Oliver Krüger

1Department of Biology and Biochemistry, University of Bath, Bath BA2 7AY, UK
2Department of Animal Behaviour, University of Bielefeld, PO Box 10 01 31, 33501 Bielefeld, Germany

In coevolutionary arms races, like between cuckoos and their hosts, it is easy to understand why the host is under selection favouring anti-parasitism behaviour, such as egg rejection, which can lead to parasites evolving remarkable adaptations to ‘trick’ their host, such as mimetic eggs. But what about cases where the cuckoo egg is not mimetic and where the host does not act against it? Classically, such apparently non-adaptive behaviour is put down to evolutionary lag: given enough time, egg mimicry and parasite avoidance strategies will evolve. An alternative is that absence of egg mimicry and of anti-parasite behaviour is stable. Such stability is at first sight highly paradoxical. I show, using both field and experimental data to parametrize a simulation model, that the absence of defence behaviour by Cape bulbuls (Pycnonotus capensis) against parasitic eggs of the Jacobin cuckoo (Clamator jacobinus) is optimal behaviour. The cuckoo has evolved massive eggs (double the size of bulbul eggs) with thick shells, making it very hard or impossible for the host to eject the cuckoo egg. The host could still avoid brood parasitism by nest desertion. However, higher predation and parasitism risks later in the season makes desertion more costly than accepting the cuckoo egg, a strategy aided by the fact that many cuckoo eggs are incorrectly timed, so do not hatch in time and hence do not reduce host fitness to zero. Selection will therefore prevent the continuation of any coevolutionary arms race. Non-mimetic eggs and absence of defence strategies against cuckoo eggs will be the stable, if at first sight paradoxical, result.

Keywords: arms race; brood parasitism; coevolution; egg acceptance; optimal behaviour

1. INTRODUCTION

Coevolution is one of the most fundamental processes producing evolutionary change [1,2]. The strong reciprocal selection pressures between predator and prey, or parasite and host, often lead to remarkable and close matching of traits in coevolving species [1,3–5]. With increasing fitness costs of parasitism, selection for host defences increases, which in turn may force parasites to specialize and evolve fine-tuned adaptations that overcome a particular host’s defences [3,5–11]. However, there are a few cases where biologists do not observe these sophisticated adaptations, but rather a lack of them [3]. As early as 1789, Gilbert White wondered why the dunnock (Prunella modularis) accepts a highly non-mimetic common cuckoo (Cuculus canorus) egg [12]. Another famous example is the failure of hosts of the common cuckoo to recognize their chicks and reject the cuckoo chick that will eventually outgrow them by a factor of 10 [13,14]. Two main hypotheses have been proposed to explain this seemingly maladaptive behaviour. The evolutionary lag hypothesis proposes that it would be advantageous for hosts to counteract brood parasitism but they do not, either because there has been insufficient time for the defence to spread through the host species population or because hosts might lack the genetic variation to evolve a defence against brood parasitism [3,13,15]. The evolutionary equilibrium hypothesis proposes that the costs of brood parasitism do not always exceed the costs of rejection and, hence, under some scenarios, it is adaptive for a host to accept brood parasitism [3]. Differentiating between these two hypotheses is extremely difficult [13].

Avian brood parasites depend entirely on hosts to raise their offspring by laying their eggs into the nests of their hosts, and hence often inflict severe fitness costs on them [2]. Owing to the high selection pressures involved, hosts have commonly evolved egg rejection of parasitic eggs, and parasites have evolved egg mimicry, sometimes so good that parasitic eggs are indistinguishable from host eggs for the human eye [8].

The Jacobin cuckoo (Clamator jacobinus) is an obligate brood parasite with three subspecies [16]. Two lay a mimetic blue egg that also matches the host eggs in size, while the subspecies in southern Africa (Clamator jacobinus serratus) parasitizes bulbuls (Pycnonotus spp.) and lays a non-mimetic white egg which is also much larger than the host eggs (figure 1a). Like in other Clamator species [17–19], the young cuckoo does not evict or kill host young but is raised with them, at least initially. The biology of the Jacobin cuckoo and its host, the Cape bulbul (Pycnonotus capensis), was studied over 12 years in two time periods (1959–1962 and 2001–2008) in the Eastern Cape, South Africa. Combining detailed observations with experiments, the aim was to test whether the evolutionary lag or evolutionary equilibrium hypothesis is the more likely explanation for the striking absence of egg rejection in this avian host–parasite system.

2. MATERIAL AND METHODS

(a) Fieldwork

I studied a population of Cape bulbuls in the nature reserve of the Nelson Mandela Metropolitan University, Eastern Cape Province, South Africa (34°01’S and 25°38’E)
between 2001 and 2008 [20]. The reserve consists of coastal sand dunes interspersed with rocky outcrops and belongs to the Cape St Francis coastal fynbos and thicket mosaic habitat [21]. The area receives around 700 mm of aseasonal rain annually. Cape bulbuls and Jacobin cuckoos were also studied by R. Liversidge at a study site similar in vegetation 3 km away between 1959 and 1962 [22] and I also used his data. Over both study periods, we have no evidence that the Jacobin cuckoo regularly parasitizes other hosts in the study area [22], but in an area only ca 5 km away but with much denser vegetation, the main host was the Greenbul (Andropadus importunus) in the 1960s, owing to low abundance of Cape bulbuls [22].

Field seasons lasted from September to December each year, coinciding with the breeding season of Cape bulbuls in this area. Fieldwork was conducted mainly from sunrise to about 10.00 h and from 15.00 h to sunset. Nests were found mostly by watching females with nest material or sometimes by following the Jacobin cuckoo, which parasitizes the Cape bulbul. Once a nest was found it was checked daily or at 2 day intervals to determine clutch size, incubation period, hatching success, nestling period and fledging success. Given that Cape bulbuls are territorial [22], repeat nesting attempts could often be determined by the position of the new nest or by the identity of the individuals, because many chicks fledged in the study area since 2002 have been banded with a unique combination of colour and metal rings. If cuckoo eggs were recorded in bulbul nests, their correct timing was assessed either by recording the day when the cuckoo egg was laid or by recording the hatching date of the cuckoo egg in relation to the hatching date of the bulbul eggs. Cuckoo eggs laid more than 2 days after clutch completion invariably failed to produce a fledgling cuckoo and this was hence used as a threshold to classify eggs as correctly or incorrectly timed.

(b) Egg discrimination experiment

During the 2001 season, I collected unhatched Cape bulbul eggs and also made Jacobin cuckoo egg models from plaster. Unhatched bulbul eggs were either added untreated to another finished bulbul clutch containing two eggs, or painted white to mimic the visible colour of a Jacobin cuckoo egg, or painted yellow to provide a completely non-mimetic and unusual stimulus. Eggs were added within 3 days of clutch completion. Added eggs were left in the host nest for at least 5 days and scored as accepted when they were still in the nest and had no scratches indicating an attempt to remove them from the nest. I also observed the initial behaviour of the female returning to her nest after the egg was added to her clutch. Each pair was tested only once. In 2004, an unhatched bulbul egg or a Jacobin cuckoo egg was added to a nest before the first egg was laid to test whether bulbuls use nest desertion as a defence strategy against cuckoo parasitism. The added egg was removed once the host laid an egg or when the nest was considered to be deserted.

(c) Grasp index measurements

Five adult specimens of Cape bulbul, jungle babbler (Turdoides striatus) and common babbler (Turdoides caudatus) were taken from the University Museum of Zoology at the University of Cambridge. I measured bill length from the commissural point at the corner of the mouth diagonally to the tip of the upper mandible. Bill breadth was measured as the distance between the commissural points. Grasp index is the product of bill length and bill breadth [23–26]. I also
collected grasp index data for other host species from the literature [15,23–26].

**Simulation model**

Ten thousand nests were initiated at random for each bulbul strategy (acceptor and deserter) between the minimum (27 August) and maximum (11 December) dates observed in the second study period (2001–2008), but with a mean initiation date as the one observed (18 October). Depending on the initiation date, predation and parasitism risks were assigned according to data presented in figure 3. The acceptor strategy made a repeat breeding attempt after a specific time delay (20 days) if predated, whereas the deserter strategy made a repeat breeding attempt with the same time delay if predated or parasitized. If predated or parasitized during the second breeding attempt, they made a third attempt after a specific time delay (20 days) but not more than three breeding attempts as this is the maximum number recorded during the study. I estimated relevant parameters from field data such as host clutch size ($n = 145$), predation risk ($n = 222$ nests), the average number of host eggs damaged (0.5) by the cuckoo egg being laid ($n = 12$ nests), host egg hatching probability ($n = 124$ eggs).

The first simulation assigned the same parasitism risk in the months October, November and December, whereas the second simulation assigned a parasitism risk in October and a parasitism risk 2.5 times higher in November and December, in line with the seasonal increase in parasitism risk observed in the field. I used the following parameter values, all estimated from field data: $C =$ clutch size (2.5), $C_p =$ parasitized clutch size (2.0), lower because a cuckoo egg cracks one bulbul egg in 50 per cent of cases ($n = 12$), $p_a =$ parasitism probability (variable), $p_r =$ predation probability (variable), $h =$ hatching probability (0.796), $t =$ cuckoo egg correct timing and hatching probability (0.6), $BC =$ probability of bulbuls to fledge with cuckoo (0.15), calculated from 13 nests, $d =$ time delay between a nest predation or nest desertion event and re-nesting (20 days), calculated from 14 accurately determined re-nesting attempts after nest failure. All programming was done in MATLAB.

3. RESULTS

(a) Breeding biology of Jacobin cuckoo and Cape bulbul

The Jacobin cuckoo parasitism rate of Cape bulbul nests varied greatly between 6 and 72 per cent per year with a mean parasitism rate of 22 per cent. Between zero and six cuckoos fledged annually from the study site. Cape bulbuls have a mean clutch size of 2.5 ($\pm$ s.e.m. = 0.04) eggs (range 1–4) and annually fledged between 0.09 and 1.05 chicks per breeding attempt with a maximum of three chicks per breeding attempt. Mean predation rate was 63.1 per cent and predation rate of parasitized nests was very similar (63.2%). On average, bulbuls fledged 0.19 ($\pm$ s.e.m. = 0.11) bulbul chicks from parasitized breeding attempts and 0.73 ($\pm$ s.e.m. = 0.08) bulbul chicks from non-parasitized breeding attempts. Hence while brood parasitism does not always reduce host fitness of the corresponding breeding attempt to zero, it greatly reduces it. While reproductive success declines significantly with laying date within a breeding season in Cape bulbuls [20], there is no such effect in Jacobin cuckoos ($r = -0.189$, d.f. = 34, $p > 0.2$). Out of a sample of 50 Jacobin cuckoo eggs where timing relative to the host could be estimated, 6 per cent were laid before host eggs were laid, 44 per cent were laid during the host laying period, 22 per cent were laid 1 or 2 days after host clutch incubation had started and 28 per cent were laid more than 2 days after host clutch incubation had started. I found that Jacobin cuckoo eggs laid more than 2 days after clutch completion and hence after host incubation has begun, failed to produce a fledgling cuckoo. The laying of the cuckoo egg damaged one host egg in ca 50 per cent of cases ($n = 12$). Jacobin cuckoo chicks outcompete host chicks normally within the first 3–5 days after host chicks hatch ($n = 11$), in most cases only one bulbul chick was outcompeted (81.8%) and rarely two (18.2%). In ca 15 per cent of cases did one bulbul chick fledge with a Jacobin cuckoo chick ($n = 13$).

(b) Jacobin cuckoo egg characteristics

Jacobin cuckoo eggs differ remarkably from Cape bulbul eggs in size, colour and shape (figure 1a). Based on literature data [16], the cuckoo egg is 93 per cent larger in volume than the host egg (6.67 versus 3.45 cm$^3$), a difference that is among the largest in any cuckoo–host system [16,27]. In addition, a simple egg-shape index, calculated after Picman [28] as (length/breadth), indicated that not only is the Jacobin cuckoo egg (shape index = 1.227) much rounder than the Cape bulbul egg (shape index = 1.402), it is the second-most round egg of all cuckoos. Only the closely related chestnut-winged cuckoo (Clamator coronandus) lays a rounder egg. The Jacobin cuckoo egg is also rounder than eggs of other avian brood parasites [28].

(c) Bulbul egg ejection and nest desertion: lack thereof

Because of the size, shape and strength of the southern African Jacobin cuckoo egg, the most plausible method of egg rejection for the Cape bulbul might be nest desertion. With a mean grasp index of 214 mm$^2$ ($n = 5$, s.e.m. = 2.64 mm$^2$), compared with a Jacobin cuckoo egg width of 22 mm, egg ejection by grasping seems unlikely (figure 1b), but cannot be ruled out. The much smaller egg of the Indian subspecies could very likely be grasped by the two main babbler hosts. In addition, the eggshell of Clamator cuckoos is particularly strong, even for cuckoo eggs which are known to have particularly strong eggshells [29]; but see also [16]. This makes egg ejection through egg puncture much harder [29] and/or more costly [3].

There is no observational evidence that Cape bulbuls eject real Jacobin cuckoo eggs [22]. Experiments showed that Cape bulbuls did not reject any egg from their nest, whether another conspecific egg, a conspecific egg painted white, Jacobin cuckoo model eggs, completely non-mimetic eggs or eggs from clutches enlarged beyond the normal range (figure 1c). Hence, the large Jacobin cuckoo egg is not a super-normal stimulus for the bulbul host [3] and this hypothesis cannot explain egg acceptance. Bulbuls also never deserted a nest after an egg was added or replaced. When conspecific eggs or cuckoo model eggs were added before the first host egg was laid, hosts sometimes deserted the nest ($n = 19$,
10.5% of cases) but there was no difference between cuckoo \((n = 12)\) and bulbul \((n = 7)\) egg treatment (Fishier's exact test, \(p = 0.509\)) and also no difference from the non-manipulated overall rate of nest desertion of the same breeding season \((n = 49, 14.3\%)\), Fishier's exact test, \(p = 0.973\). As the background rate of desertion of non-parasitized nests before egg laying was much lower across years \((n = 145, 3.4\%)\), desertions witnessed in the experiment are unlikely to simply reflect the background rate of desertion before egg laying. In conclusion, while bulbuls never eject an egg, they are capable of nest desertion but do not use this strategy as a defence against brood parasitism. Why could this be?

**Should bulbuls desert the nest or accept the cuckoo egg?**
The costs of desertion should be relatively low, as only time and the resources that went into the eggs are wasted. However, another peculiarity of Jacobin cuckoos is that they regularly fail to hatch on time and/or they are often laid too late (i.e. well after host incubation has begun). Over the 12 years of fieldwork, only 60 per cent of cuckoo eggs were correctly timed and fertile, based on the known laying date and hatching rate of 50 cuckoo eggs. The estimated probability of correct timing was 72 per cent and hatching rate was estimated at 83.3 per cent. In some cases the timing was so bad that cuckoo eggs were laid up to 16 days after the host clutch was completed, when bulbul chicks were around 3 days old [22]. If a cuckoo hatched at all from mistimed eggs (i.e. eggs laid more than 2 days after host clutch incubation has begun), it had no chance of competing with the host chicks [22]. I formulated a simulation model to calculate the fitness pay-offs over a breeding season for an acceptor strategy and a deserter strategy (figure 2, see methods and figure legend for abbreviations). Another crucial aspect of the breeding biology of the Cape bulbul is the marked increase in both parasitism and predation rate over the breeding season that lasts from late August to December at the study site (figure 3). Nests are initiated on average on the 18 October \((s. e. m = \pm 1.5\) days). Early nests initiated in late August and September have no parasitism risk, as Jacobin cuckoos arrive at the study site in late September or early October [20,22], nests initiated in October have a 16 per cent chance of being parasitized while nests initiated in November and December have a 40 per cent chance of being parasitized. Predation risk triples between August and September, increases to over 70 per cent for the months of October and November and nearly all nests are parasitized in December. There was no significant difference in predation rate between parasitized \((63.2\%\) predated) and non-parasitized nests \((63.1\%\) predated, \(\chi^2 = 0.001, d.f. = 1, p > 0.95\)). The parameters of the simulation model (figure 2) were all estimated from field data. Depending on the generated nest initiation date, predation and parasitism risks were assigned according to data presented in figure 3. The model then estimated the mean seasonal fitness of both the acceptor and deserter strategy numerically using the probabilistic framework as specified by the probability bifurcations shown in figure 2.

Regardless of parasitism rate, the acceptor strategy always yields a higher fitness than the deserter strategy and at the mean annual parasitism rate observed over the 12 years \((0.22)\), the difference in fitness is 8.2 per cent (figure 4a). Perhaps counterintuitively, with increasing brood parasitism rate, the fitness advantage of the acceptor strategy becomes larger. However, nest desertion is so costly given the time delay and the increasing parasitism and predation risk over the season that it is optimal to make the best of a bad job if bulbuls are parasitized.

It might be argued that the time delay of 20 days used in the model between a predated or deserted breeding attempt and a second breeding attempt is much longer

**Figure 2.** Probability tree for egg (a) acceptors and (b) deserters. Abbreviations are \(C =\) clutch size (2.5), \(C_p =\) parasitized clutch size (2.0), lower because a cuckoo egg cracks one bulbul egg in 50% of cases \((n = 12\) nests), \(pa =\) parasitism probability (variable), \(pr =\) predation probability (variable), \(0 =\) zero, \(h =\) hatching probability (0.796), \(t =\) cuckoo egg correct timing probability (0.6), \(BC =\) probability of bulbuls to fledge with cuckoo (0.15), calculated from 13 nests, \(d =\) time delay between a nest predation or nest desertion event and re-nesting (20 days), calculated from 14 accurately determined re-nesting attempts after nest failure at the incubation stage. Both strategies made a maximum number of three breeding attempts per season.
than in temperate species, although this is a parameter that has been measured in the field. Artificially reducing the time delay to the second breeding attempt after a failed or deserted breeding attempt to 10 days does not, however, change the conclusions qualitatively: at the parasitism rate observed over the 12 years (0.22), the difference in fitness between the acceptor and deserter strategy is still 7 per cent. If parasitism rates follow the seasonal increase exactly as observed in the real population (parasitism rates in November and December are 2.5 times as high as the parasitism rate in October), the acceptor strategy also yields a higher fitness compared with the deserter strategy (figure 4b).

These consistent differences arise because deserters would sometimes desert a parasitized clutch with a cuckoo egg, which would fail to hatch or would hatch too late, and hence desert a valuable clutch. As parasitism probability increases, this error increases in frequency, hence increased brood parasitism puts a progressively stronger selection pressure on the host not to desert. The proportion of correctly timed cuckoo eggs seems crucial for the acceptor strategy to yield a higher fitness, but the advantage of the acceptance behaviour is strikingly resilient to changes in parameter settings. A sensitivity analysis shows that at 10 per cent parasitism rate, 80 per cent of cuckoo eggs need to be timed correctly for the deserter strategy to yield a higher fitness and at a parasitism rate of 20 per cent, over 90 per cent of cuckoo eggs need to be timed correctly for the deserter strategy to be selected for (figure 4c). Hence even if considerably more cuckoo eggs were timed correctly, the acceptor strategy would be selected for at current levels of brood parasitism because the Jacobin cuckoo chick fledges alongside a host young in ca 15 per cent of successfully parasitized nests.

4. DISCUSSION
The result that an increasing brood parasitism rate increases the selection pressure on the host not to evolve a defence is paradoxical at first. Effectively, selection will prevent Cape bulbuls from entering a coevolutionary arms race with the Jacobin cuckoo. This suggests that the evolutionary equilibrium hypothesis can explain what initially seemed to be a clear case of evolutionary lag: complete absence of host defences against brood parasitic eggs. This might be due either to the bulbul host not being able to eject the cuckoo
egg from the nest and nest desertion being too costly or, alternatively, costs of brood parasitism are sufficiently low to prevent the escalation of the arms race. A similar case has been reported from the closely related great spotted cuckoo (Glama tor glandarius) where one of its hosts, the carrion crow (Corvus corone), does not show any defence behaviour [19,30,31]. This is apparently most likely explained by the low costs of parasitism in this particular system [31]. Likewise, the case of the defenceless dunnock being parasitized by non-mimetic eggs of the common cuckoo is probably best explained by low costs owing to low parasitism frequency [3]. The very high predation rates (63%) in this study effectively prevent brood parasitism from being very costly but nevertheless parasitized bulbul breeding attempts fledge only 0.2 bulbul chicks on average while non-parasitized breeding attempts fledge 0.7 bulbul chicks on average, so the costs of parasitism for individuals are substantial. This suggests to me that low costs of parasitism are not the most likely explanation for the lack of defences of Cape bulbuls.

An important question is whether the peculiar features of the Jacobin cuckoo egg evolved specifically to make egg ejection harder or whether they are a by-product of other selection pressures [32,33]. Jacobin cuckoo females often lay their eggs by dropping them into the nest, sometimes from over 10 cm height [22], so the round shape of the egg and its particularly strong eggshell have most likely evolved to avoid laying damage [34,35]. This is often the only way to lay as the fierce aggregation of bulbuls against Jacobin cuckoos near their nests makes egg-laying very difficult but leads to breakage of a host egg in roughly 50 per cent of cases. The process often involves cooperation between male and female Jacobin cuckoos and can take over 2 h to accomplish [22].

While the southern African subspecies of Jacobin cuckoo lays non-mimetic eggs that are much larger than expected for its body size [27], the Indian subspecies lays smaller but mimetic eggs. The Indian subspecies evolved egg mimicry in coloration and size to overcome host defences. In contrast, by laying a very large and especially round egg, the southern African subspecies has made grasp ejection as a means of rejection unlikely. The bulbul host shows a high level of aggression against the Jacobin cuckoo and investment in this first line of defence might reduce selection in the second line of defence, egg rejection [36]. However, other cuckoo hosts show both high levels of aggression against the cuckoo as well as highly developed egg-ejection abilities [37]. I can only hypothesize that one consequence of the high aggression shown by bulbuls might be a high proportion of mistimed cuckoo eggs as cuckoo females could be prevented from laying their eggs at an appropriate time. Such a mechanism has also been invoked to explain the less accurate timing of great spotted cuckoo eggs in cooperatively breeding carrion crows [19].

Nest desertion seems to be the most workable option for the bulbul host once the cuckoo egg is laid. This option is normally much less beneficial than egg ejection for hosts of brood parasites [35], but in this case it is suboptimal and leads to no coevolution and the southern African subspecies of Jacobin cuckoo is under no selection pressure to evolve egg mimicry.

A similarly paradoxical case of parasite–host coevolution to the one presented here has been described by Lyon & Eadie [38] in the black-headed duck (Heteronetta atricapilla). While hosts have evolved egg rejection as a response to conspecific brood parasitism, the interspecific parasite has not evolved egg mimicry and lays a plain white egg. Given that hosts can discriminate between their own eggs and those laid by another female of the same species, any incremental change in the appearance of the duck’s egg would not increase the chance of acceptance by the hosts, so coevolution cannot get started. Hence, not responding to a coevolutionary arms race is the optimal behaviour. Similarly, some models in economics [39] suggest that if potential costs are very high, the optimal strategy may be to refrain from maximizing economic growth.

In conclusion, a seemingly obvious case of evolutionary lag where either host or parasite fail to evolve in the face of strong selection exerted by the other party can reveal much about constraints of coevolutionary arms races [40]. Behaviour thought to be lagging behind may turn out to be optimal given the operating constraints, thus underlining the importance of evolutionary equilibrium in animal behaviour. Evolutionary lag arguments should not be accepted on plausibility grounds alone and should not serve as a fall-back hypothesis which is often very difficult to falsify [41].

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