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The evolution of egg size in the brood parasitic cuckoos

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We compared genera of nonparasitic cuckoos and two groups of parasitic cuckoos: those raised together with host young ("nonejectors") and those in which the newly hatched cuckoo either ejects the host eggs or chicks, or kills the host young ("ejectors"). Nonejectors are similar to their hosts in body size and parasitize larger hosts than do ejectors, which parasitize hosts much smaller than themselves. In both types of parasite, the cuckoo's egg tends to match the host eggs in size. To achieve this, nonejectors have evolved a smaller egg for their body size than have nonparasitic cuckoos, and ejectors have evolved an even smaller egg. Among ejector cuckoo genera, larger cuckoos have larger eggs relative to the eggs of their hosts, and the relationship between cuckoo egg volume (mass of the newly-hatched cuckoo) and host egg volume (mass to be ejected) did not differ from that predicted by weight-lifting allometry. However, comparing among *Cuculus* cuckoo species, the allometric slope differed from the predicted, so it is not clear that egg size is related to the need to give the cuckoo chick sufficient strength for ejection. Comparing the two most speciose ejector genera, *Chrysococcyx* cuckoos (smaller and parasitize dome-nesting hosts) lay eggs more similar in size to their host's eggs than do *Cuculus* cuckoos (larger and parasitize open cup–nesting hosts). Closer size-matching of host eggs in *Chrysococcyx* may reflect the following: (1) selection to reduce adult body mass to facilitate entry through small domed nest holes to lay, and (2) less need for a large egg, because longer incubation periods in dome-nesting hosts allow the young cuckoo more time to grow before it need eject host eggs. *Key words:* brood parasitism, cuckoo, egg size, host nest architecture. *[Behav Ecol 15:210–218 (2004)]*

Among the cuckoos (family Cuculidae), 53 of the 136 species are obligate brood parasites and always lay their eggs in the nests of other species, which act as hosts, incubating the parasite's eggs and then raising the parasitic chicks to independence. The other 83 cuckoo species raise their own young, just like normal nesting birds (Payne, 1997). Cuckoo-host interactions have proved to be a good model system for studying coevolution (Davies, 2000; Rothstein, 1990). Hosts have evolved defenses in response to parasitism (aggression against the parasite, egg rejection), whereas cuckoos, in turn, have evolved tricks to beat host defenses (secretive laying, egg mimicry). Here, we consider how a parasitic life history has influenced the evolution of cuckoo egg size.

Payne (1974) showed that parasitic cuckoo species lay smaller eggs than do nesting cuckoo species of the same body mass. He suggested that parasitic cuckoos increased their egg laying opportunities by choosing host species smaller than themselves, because these tend to be more abundant than are larger hosts. Once small hosts are chosen, it might pay the cuckoo to lay a small egg, one that matches the host eggs in size, both to increase the chance of acceptance and to facilitate incubation (Payne, 1974). These ideas were anticipated by Darwin (1859) in *The Origin of Species*, who commented on the unusually small egg laid by the common cuckoo (*Cuculus canorus*). This is a 100 g bird that parasitizes small warblers, pipits, and shrikes (10–30 g), and it lays a 3 g egg, compared with a 10 g egg laid by a nesting cuckoo of the same body size (Payne, 1974). Darwin wrote, "the eggs are remarkably small, not exceeding those of the skylark" (*Alauda arvensis*, 35 g), and he suggested this was advantageous "to deceive certain foster parents or ... to hatch within a shorter period."

Recent experiments have confirmed that hosts discriminate against foreign eggs larger than their own (Davies and Brooke, 1988; Marchetti, 2000; Mason and Rothstein, 1986), and a comparative analysis, using independent contrasts from two cuckoo phylogenies, has shown that the evolution of parasitism is indeed correlated with the evolution of decreased egg size (Krüger and Davies, 2002). Our aim in this article is to explore further the evolution of egg size in parasitic cuckoos by examining how it is related to host size and parasitic strategy.

First, we compare two groups of parasitic cuckoos, namely, those that are raised together with the host young (the "nonejectors") and those in which the newly-hatched cuckoo either ejects the host eggs or chicks, or kills the host young, and so is raised alone in the nest (the "ejectors"; see Table 1). We explore the influence of these different strategies on choice of host size and on the relationships between cuckoo egg size and body size. Nonejector cuckoos have to compete for food with the host young, whereas ejector cuckoos need the strength to eject host eggs or chicks. We test whether the increase in egg size among ejector cuckoos that parasitize larger hosts can be explained by weight-lifting allometry (McMahon and Bonner, 1983), namely, the need to lay an egg of a sufficient size to give the newly hatched cuckoo the strength to eject the host eggs from the nest.

Second, we examine the influence of host nest architecture by comparing the two most speciose parasitic cuckoo genera. *Cuculus* cuckoos exploit hosts with open-cup nests, in which small body size is not so essential to facilitate laying because the cuckoo either sits briefly on the host nest or perches on the rim to lay (Davies, 2000). By contrast, *Chrysococcyx* cuckoos exploit hosts with domed nests, and they go right inside through the small entrance holes in order to lay (Brooker et al., 1988; Rowan, 1983). Their hosts include weaverbirds and sunbirds in Africa and Asia (Rowan, 1983), as well as fairy wrens and thornbills in Australia (Brooker and Brooker, 1989). We test whether this difference in host nest architecture has consequences for cuckoo body size and cuckoo egg size. Specifically, we test two ideas: (1) adult *Chrysococcyx* cuckoos might need to be small to enter the domed nests of

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Table 1

Parasitic cuckoo species that are raised either alongside the host young (nonejectors) or alone, because they kill the host chicks or eject the host eggs or chicks (ejectors)

Nonejectors	Ejectors
Clamator (4 species)	*Pachycoccyx* (1 species)
Eudynamys scolopacea	*Cuculus* (16 species)
Scythrops novaehollandiae	*Cercococcyx* (3 species)
	Cacomantis (6 species)
	Rhamphomantis (1 species)*
	Chrysococcyx (12 species)
	Caliechthrus (1 species)
	Surniculus (2 species)
	Microdynamis (1 species)
	Eudynamys (2 species)
	Tapera (1 species)†
	Dromococcyx (2 species)†

Classification after Payne (1997).

* No information on breeding biology, so excluded from our analysis.

† In *Tapera*, and probably also *Dromococcyx*, the newly-hatched cuckoo chick kills the host young. In all the others in this column, the cuckoo chick ejects the host eggs or young.

their hosts, with resulting consequences for their egg size. (2) The longer incubation period commonly found in hole-nesting birds (Lack, 1968) might allow *Chrysococcyx* cuckoos to lay relatively smaller eggs than do *Cuculus* cuckoos, because the young *Chrysococcyx* cuckoo would hatch further in advance of the host young and so would have more days to grow and gain strength before it need eject the host eggs.

METHODS

An analysis of the relationship between cuckoo body mass and egg size (or host size) using all cuckoo species as data points could be biased by a few cuckoo genera with a large number of species (Table 1), which may share characteristics through common descent, and so these would not be independent evolutionary events (Harvey and Pagel, 1991). Furthermore, comparisons of slopes of cuckoo size/egg size relationships would be difficult to interpret; it is well known that slopes tend to be higher when calculated across more phylogenetically diverse groups than across more closely related groups, because intercepts often vary between taxonomic groups (Harvey and Mace, 1982). Because there is currently no complete cuckoo phylogeny available to permit a contrast analysis, we have tried to minimize these problems by using mean values per cuckoo genus. We have shown previously that there are marked differences between nesting and parasitic cuckoo genera in both body size and egg size (Krüger and Davies, 2002). The raw data are summarized in the Appendix and were derived from Brooker and Brooker (1989), Payne (1997), Rowan (1983), and Schönwetter (1967–1992). For cuckoos that parasitize several host species, we have used mean values for host mass and host egg volume. In our comparison of *Cuculus* and *Chrysococcyx* cuckoos, we focus on adaptive radiation within a genus, in which cross-species comparisons can be informative and as valid as contrast analyses (Harvey and Rambaut, 2000; Price, 1997). Because of missing data for some species, the number of species included in the analyses can differ from the total given in Table 1.

We report results using ordinary least-square regressions, instead of major axis regressions, because the error variance in our predictor variable (body mass) could be assumed to be less than that in the dependent variable (egg volume, host mass). In such scenarios, ordinary least-square regression is justified (McArdle, 1988; Rayner, 1985; Ricklefs, 1996; Weathers and Siegel, 1995). The difference in error variances is caused by the fact that cuckoo species commonly parasitize more than one host, so by using an average host body mass and host egg volume for a given cuckoo species, we obviously increase the measurement error in comparison to that of cuckoo mass. The same applies to the relationship between cuckoo body mass and cuckoo egg volume, because egg volume was estimated by using measurements of egg length and breadth, following the formula of Hoyt (1979), egg volume $= 0.51 \times$ egg length $\times$ egg breadth^2, and hence has a much larger error variance than body mass. Before analysis, variables were log-transformed to achieve normality. We also computed major axis regressions. Although this obviously changed the values of the slopes, in no case did our main conclusions differ from those with least-square regression. All statistical tests are two-tailed. Because sample sizes for our comparisons are small, we have conducted power tests to see whether nonsignificant difference become significant if a minimum sufficient power (0.7, Zar, 1999) was reached. No comparison between slopes became significant at a power level of 0.7, so our negative results are robust.

In the cuckoo genera and species analyses, we have followed the nomenclature of Payne (1997), so the genus *Clamator* includes *Oxylophus*, the genus *Chrysococcyx* includes *Misocalius* and *Chalcites*, the genus *Cacomantis* includes *Penthoceryx*, and the genus *Eudynamys* includes *Urodynamys* (Table 1).

RESULTS

Comparing egg size in nesting and parasitic cuckoos

Egg size increased with body size for genera of nonparasitic cuckoos and for genera of the two parasitic cuckoo strategies, namely, nonejectors and ejectors (Figure 1). There were no differences in slopes between these three regressions, but clear differences in elevation. For a given body mass, nonparasitic cuckoo genera laid significantly larger eggs than did both nonejector and ejector parasitic cuckoos. Within the parasitic cuckoos, ejector cuckoos laid much smaller eggs for a given body mass than did nonejectors.

Comparing host size and matching of host egg size in parasitic cuckoos

Among both nonejector and ejector cuckoo genera, larger cuckoos parasitize larger hosts (Figure 2). However, there are marked differences between them in host size relative to cuckoo size. Although nonejectors parasitize hosts similar in size to themselves, ejector cuckoos are much larger than their hosts (Figure 2). Nevertheless, in both types of parasite, the cuckoo egg tends to match the host's egg in size (Figure 3). For ejector cuckoo genera, the slope in Figure 3 is significantly less than one, which means that the larger the cuckoo, the larger the cuckoo egg relative to the host egg (see section after next).

Comparing host size in *Cuculus* and *Chrysococcyx* cuckoos

We now compare cuckoo species within the two most speciose cuckoo genera. *Chrysococcyx* cuckoos, which parasitize dome-nesting hosts, are clearly much smaller than are *Cuculus* cuckoos, which parasitize open cup–nesting hosts (Figure 4a; no overlap in body mass between species in these two cuckoo genera). On average, *Chrysococcyx* cuckoos exploit smaller hosts than do *Cuculus* cuckoos ($F_{1,20} = 6.001$, $p = .024$). Within both genera, larger cuckoo species parasitize larger

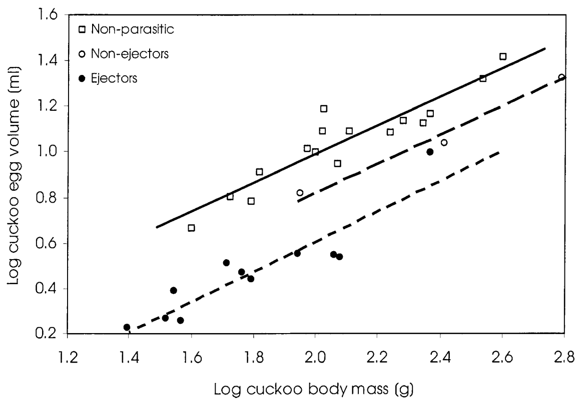

Figure 1
Relationship between mean body mass and mean egg volume for 16 nonparasitic cuckoo genera ($y = 0.633x - 0.280$; $r^2 = .864$; $F_{1,14} = 88.701$, $p < .0001$), three nonejector parasitic cuckoo genera ($y = 0.600x - 0.372$; $r^2 = .980$; $F_{1,1} = 48.598$, $p = .091$), and 11 ejector parasitic cuckoo genera ($y = 0.670x - 0.731$; $r^2 = .849$; $F_{1,9} = 50.658$, $p < .0001$). There were no significant differences in slopes of the regression lines (nonparasitic versus nonejectors $t_{15} = 1.442$, $p = .170$; versus ejectors $t_{23} = 1.573$, $p = .129$; nonejectors versus ejectors $t_{10} = 1.625$, $p = .135$). There were significant differences in elevation in all three lines (nonparasitic versus nonejectors $t_{16} = 4.620$, $p < .001$, versus ejectors $t_{24} = 4.435$, $p < .001$; nonejector versus ejectors $t_{11} = 2.607$, $p < .05$).

host species, but the most striking difference is that *Chrysococcyx* cuckoos are much smaller than are *Cuculus* cuckoos even when they exploit similar-sized hosts (Figure 4a).

We have included the nonejector cuckoos for comparison in Figure 4. There are seven taxa plotted here because *Clamator jacobinus* has two distinct subspecies that differ in their host size (see Appendix). Although, on average, nonejector cuckoos are similar in body mass to their hosts, *Chrysococcyx* cuckoos are about twice the mass of their hosts, whereas *Cuculus* cuckoos are over four times the mass of their hosts (Figure 4b).

On average, nonejector cuckoos are similar in body mass to their hosts across all their range of cuckoo body sizes (Figure 4a: slope not significantly different from one, $t_5 = 2.229$, $p = .076$). However, the mass difference between cuckoo and host becomes increasingly marked both for smaller *Cuculus* and smaller *Chrysococcyx* species (slopes in Figure 4a significantly greater than one; $t_{11} = 11.456$, $p < .001$ and $t_7 = 28.437$, $p < .001$, respectively).

Cuckoo weight lifters?

Could the slope of increase in cuckoo size with host size among ejector cuckoos reflect the need for the female cuckoo to lay an egg large enough to give its newly hatched chick sufficient strength to eject the host eggs? Strength is proportional to the cross-sectional area of muscle or torso, so in theory strength is predicted to increase in proportion to the two-thirds power of body mass (McMahon and Bonner, 1983). Therefore, the mass that an individual can lift is given by $y = km^{2/3}$, where m is the body mass of the lifter and k is a constant. This means the larger the individual, the smaller the proportion of its own body mass that it can lift. The world records for humans in weight-lifting championships fit this prediction closely: log weight lifted increases with a slope of 0.675 when plotted against log body weight of the athlete (Lietzke, 1956).

An ejector cuckoo balances each host egg on its back, one by one, and heaves them out of the nest, resting between each load. The cuckoo chick's task is similar to that of the human weight lifter; it needs body strength to support the host egg, leg strength to carry the load up to the nest rim, and arm (wing stub) strength to lift the egg overboard. If cuckoo egg size is constrained by weight-lifting allometry, then as host egg size increases, cuckoo eggs would have to become relatively larger so that the newly hatched cuckoo has sufficient strength for ejection.

To test this, we plotted cuckoo egg volume (a measure of the mass of the newly hatched cuckoo) against host egg volume (a measure of the mass the cuckoo has to lift each time). Comparing across cuckoo genera, the slope of the increase in log host egg volume with increase in log cuckoo egg volume is 0.747 (Figure 3), which is not significantly different from the predicted slope of two-thirds ($t_9 = 1.682$, $p = .127$). The key comparison is with the nonejector cuckoos, but unfortunately, there are only three genera. Nevertheless,

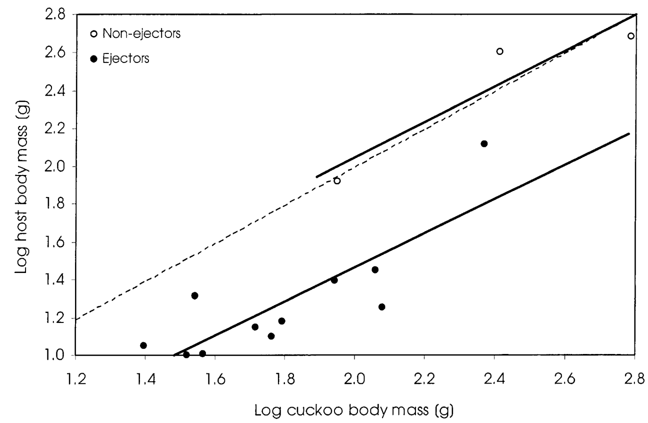

Figure 2
Relationship for parasitic cuckoos between mean cuckoo body mass and mean host body mass for three nonejector cuckoo genera ($y = 0.936x + 0.169$; $r^2 = .872$; $F_{1,1} = 6.833$; $p = .233$) and for 11 ejector cuckoo genera ($y = 0.897x - 0.336$; $r^2 = .689$; $F_{1,9} = 19.915$; $p = .002$). No significant difference in slopes ($t_{10} = 0.678$, $p = .528$), but elevations differ ($t_{11} = 2.792$, $p < .02$). Dashed line is $y = x$.

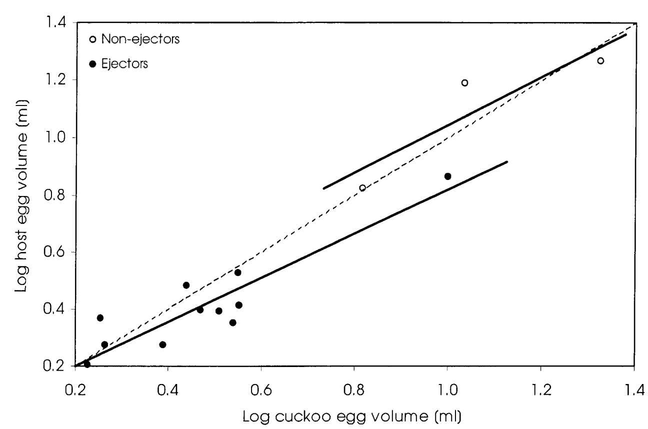

Figure 3
Relationship between cuckoo egg volume and mean host egg volume for three nonejector cuckoo genera ($y = 0.842x + 0.200$; $r^2 = .814$; $F_{1,1} = 4.387$; $p = .284$) and for 11 ejector cuckoo genera ($y = 0.747x + 0.059$; $r^2 = .823$; $F_{1,9} = 41.944$; $p < .001$). Dashed line is $y = x$. Slope for nonejectors does not differ significantly from one ($t_1 = 2.094$, $p = .284$), whereas slope for ejectors does differ significantly from one ($t_9 = 5.526$, $p < .001$).

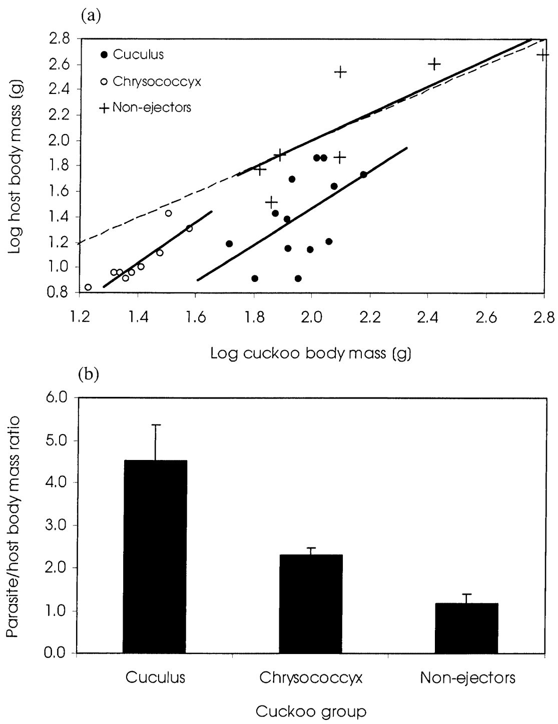

Figure 4
(a) Average host mass plotted against cuckoo mass for nine *Chrysococcyx* cuckoo species and 13 *Cuculus* cuckoo species. In both genera, larger cuckoo species parasitize larger hosts; for *Chrysococcyx* $F_{1,7} = 25.862$, $p < .001$, for *Cuculus* $F_{1,11} = 4.377$, $p = .060$. The regression line for *Chrysococcyx* is significantly steeper ($t_{18} = 2.234$, $p < .05$). The data for the seven nonejector cuckoo taxa are included for comparison. The dashed line is $y = x$. (b) Mean ($\pm$SE) parasite-host body mass ratios differ across the three cuckoo groups ($F_{2,26} = 6.737$, $p = .004$). *Cuculus* differ from *Chrysococcyx* ($p = .049$) and nonejectors ($p = .005$; Tukey-tests), but there is no difference between *Chrysococcyx* and nonejectors ($p = .539$).

it is encouraging for the theory that the slope does not differ significantly from one ($t_1 = 2.094$, $p = .284$), whereas that for the ejector cuckoos is significantly less than one (Figure 3).

However, when we considered the relationship between cuckoo egg volume and host egg volume for species within the two most speciose ejector cuckoo genera (Figure 5), the slope differs between *Cuculus* and *Chrysococcyx* cuckoos ($t_{18} = 5.329$,

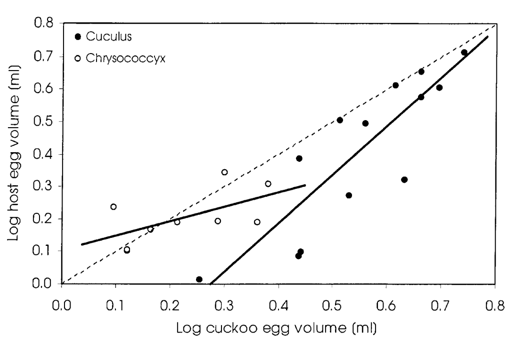

Figure 5
Comparison of host egg volume and cuckoo egg volume for *Chrysococcyx* species ($y = 0.455x + 0.099$, $r^2 = .371$, $F_{1,7} = 4.125$, $p = .082$) and *Cuculus* species ($y = 1.490x - 0.415$, $r^2 = .742$, $F_{1,11} = 31.609$, $p < .0001$). Slopes differ significantly ($t_{18} = 5.329$, $p < .001$). The dashed line is $y = x$.

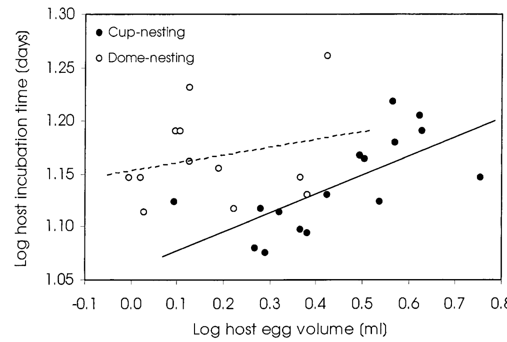

Figure 6
Relationship between host egg volume and incubation time for cup-nesting and dome-nesting hosts of *Cuculus* and *Chrysococcyx* cuckoos. Each point is a genus mean from parasitized host species. For cup-nesting hosts, $y = 0.178x + 1.060$; $r^2 = .476$; $F_{1,14} = 12.698$; $p = .003$. For dome-nesting hosts, $y = 0.074x + 1.153$; $r^2 = .059$; $F_{1,10} = 0.625$; $p = .448$. No significant difference in slopes ($t_{24} = 0.125$), but elevations differ ($t_{25} = 2.759$; $p < .02$).

$p < .001$). For *Chrysococcyx*, the slope is 0.455, significantly less than one ($t_7 = 4.572$, $p < .005$) and does not differ from the predicted 0.67 ($t_7 = 1.804$, $p = .114$), whereas for *Cuculus* the slope is significantly greater than one ($t_{11} = 8.196$, $p < .001$) and, hence, much steeper than that predicted from weight-lifting allometry.

We examine some possible explanations for the differences between *Cuculus* and *Chrysococcyx* cuckoos in the next section.

Comparing egg size in *Cuculus* and *Chrysococcyx* cuckoos

Chrysococcyx cuckoos lay eggs that are a closer size match to their host's eggs than do *Cuculus* cuckoos (Levene test for equality of variances in cuckoo-host egg ratios: $F_{1,20} = 4.286$, $p = .046$) (Figure 5). We consider two hypotheses to explain this.

Hypothesis 1: dome-nesting hosts may have longer incubation periods

Open cup-nesting birds often suffer heavy nest predation, so selection has favored short incubation and nestling periods to reduce the period when eggs and chicks are vulnerable (Bennett and Owens, 2002; Conway and Martin, 2000; Lack, 1968). If domed nests are safer, then there would be less selection for rapid development, and hence, incubation periods might be longer. This difference would have important implications for a cuckoo, because with a dome-nesting host, there would be less pressure to hatch early, to be in time to eject the host eggs (likely to be an easier task than ejecting host chicks). Therefore, *Chrysococcyx* cuckoos could get away with an egg no bigger than the host eggs, because their cuckoo chick would hatch well ahead of the host young and so have several days to grow before it needed to eject the host eggs. *Cuculus* cuckoos, by contrast, would hatch less in advance of the host eggs and so would need to eject at a younger age. Their relatively larger eggs may be necessary to provide the newly-hatched cuckoo with sufficient strength for its task.

To test whether dome-nesting hosts have longer incubation periods, we regressed incubation time against egg size, because incubation period is known to be longer for larger eggs (Rahn and Ar, 1974; Starck and Ricklefs, 1998). For a given egg size, the eggs of dome-nesting hosts do indeed have longer incubation periods than those of open cup–nesting hosts (Figure 6). This may help to explain why *Cuculus canorus*, hatching from an egg a little larger than the host eggs (Moksnes and Røskaft, 1995), usually ejects the host eggs within 1 day of hatching, whereas *Chrysococcyx* cuckoos, hatching from eggs more similar in size to the host eggs, often hatch several days before the host eggs and delay ejection until they are 2 to 4 days old (Davies, 2000; Rowan, 1983).

Hypothesis 2: Chrysococcyx cuckoos may more closely match their host eggs in size simply because they are more similar to their hosts in body size

According to this hypothesis, the closer size matching of the host eggs is simply a consequence of selection for smaller body size in *Chrysococcyx* cuckoos. We calculated egg mass as a proportion of body mass and regressed this against body mass, both for the cuckoos and for their hosts (Figure 7). As has been shown for other bird taxa (Rahn et al., 1975; Starck and Ricklefs, 1998), smaller species of cuckoos and hosts lay relatively larger eggs in proportion to their body mass. We compared the residuals in Figure 7 and found no significant difference between *Cuculus* and *Chrysococcyx* ($t_{20} = 0.133$, $p = .896$) or between their hosts ($t_{20} = 0.256$, $p = .801$). Therefore, *Chrysococcyx* have not evolved an unusual egg size relative to their body size; the closer size match of their eggs to their host's eggs comes about simply because *Chrysococcyx* cuckoos are a closer match in body size to their hosts than are *Cuculus* cuckoos (Figure 4). This is likely to reflect selection for smaller body size in *Chrysococcyx*, to enable them to enter the domed nests of their hosts to lay.

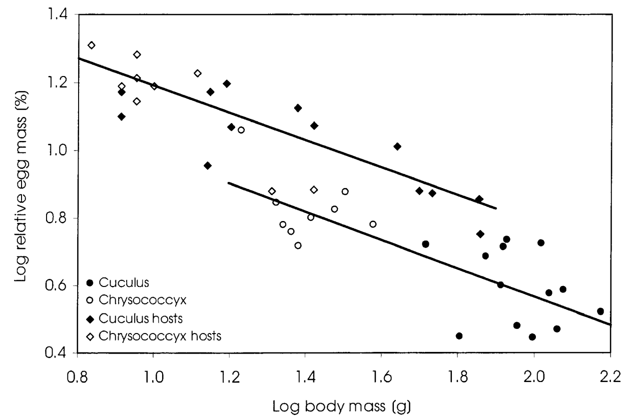

Figure 7
Relationship between body mass and egg mass relative to body mass for *Chrysococcyx* and *Cuculus* cuckoos ($y = -0.408x + 1.395$, $r^2 = .614$, $F_{1,20} = 31.814$, $p < .001$) and their hosts ($y = -0.408x + 1.582$, $r^2 = .713$, $F_{1,20} = 49.796$, $p < .001$). Slopes do not differ significantly between the two ($t_{40} = 0.067$, $p = .947$).

DISCUSSION

Most parasitic cuckoos lay one egg per host nest, and their young are then raised alone (Payne, 1997, see also Table 1). We showed that these "ejecting" cuckoos are in general larger than their hosts in body size (Figure 2). By contrast, the nonejecting cuckoos, whose young are raised together with the host young, in general parasitize hosts that are similar in body mass to themselves (Figure 2).

Two factors could explain why cuckoos that exploit relatively large hosts do not eject (Davies, 2000). The first is that beyond a certain size limit, the host eggs or chicks could simply be relatively too large for a newly hatched cuckoo chick to eject, so having to compete with host young is the price to be paid for exploiting relatively larger hosts. Two of our results suggest that the cuckoo chick's ejection performance might indeed be constrained by egg size: (1) the delayed ejection in at least some *Chrysococcyx* cuckoos suggests that it is advantageous for the young cuckoo to gain strength before it ejects when longer incubation periods for host eggs permit a delay; and (2) among ejector cuckoo genera, larger cuckoos have larger eggs relative to their host eggs, and this relationship does not differ from that predicted by weight-lifting allometry (Figure 3). Therefore, as hosts increase in size, a point may be reached at which the cuckoo's egg has to be so much larger compared with the host egg (to give the newly hatched cuckoo sufficient strength for ejection) that the hosts would easily recognize it was foreign and eject it. Hence, cuckoos that exploit large hosts would be forced to be nonejectors.

However, there was considerable variation around the cuckoo genera regression line in Figure 3, and when we compared among *Cuculus* species, we found the opposite trend—smaller cuckoo species have larger eggs relative to host eggs, the reverse of that predicted by the weight-lifting argument. We conclude that the evidence for weight-lifting as a constraint on ejector cuckoo egg size is not strong. Several other studies have found that allometric exponents vary with the taxonomic level of analysis, and it is not always clear how to interpret this (Bennett and Owens, 2002).

The second factor potentially explaining why cuckoos with relatively large hosts do not eject is that the large nests of these hosts provide room for more than one parasite chick so, unlike ejecting cuckoos, females of nonejecting cuckoo species sometimes lay two or more eggs in the same host nest (Martinez et al., 1998; Payne, 1974). Thus, nonejection may be favored by kin selection. Given that nonejector chicks face competition with host chicks, other mechanisms have evolved to monopolize foster-parental care. Nonejector chicks usually win the competition for food and grow faster than the host chicks, by means of their more exuberant begging displays (Lichtenstein, 2001; Redondo, 1993; Soler et al., 1995).

We found that in all parasitic cuckoos, the cuckoo's egg tends to match the host egg in size (Figure 3). This is likely both to increase the chance that the hosts accept the parasitic egg (Davies and Brooke, 1988; Marchetti, 2000; Mason and Rothstein, 1986) and to improve its incubation efficiency (Davies and Brooke, 1988; Payne, 1974). We found that nonejector cuckoos have evolved a slightly smaller egg for their body size than have nonparasitic cuckoos (Figure 1). However, the most marked decrease in egg size is in the ejector cuckoos (Figure 1), which exploit hosts so much smaller than themselves. These two results confirm the earlier findings of Payne (1974). On average, smaller species are more abundant than are larger species (Brown, 1995), so the exploitation of small hosts will increase egg-laying opportunities (Payne, 1974). Another advantage of smaller eggs might be that the parasitic cuckoo is effectively spreading its risk by laying a higher number of smaller eggs compared with a smaller number of large eggs (Payne, 1977). Finally, it may also be easier for a parasite to withstand attacks from smaller hosts when it approaches host nests.

We showed that the comparison of the two most speciose genera of ejector cuckoos revealed the influence of host nest architecture on cuckoo parasitism. *Chrysococcyx* cuckoos are smaller in body size than are *Cuculus* cuckoos, and this is true even when they parasitize hosts of similar body size (Figure 4a). We suggest that this smaller size in *Chrysococcyx* cuckoos has evolved to enable them to enter their hosts' domed nests to lay. By contrast, *Cuculus* cuckoos mainly exploit hosts with open-cup nests, in which small body size is not so essential to facilitate laying. In support of this interpretation, the only two *Cuculus* cuckoos that favor dome-nesting hosts are the two smallest in the genus, the Asian lesser cuckoo *C. poliocephalus* (52 g) and the Madagascar lesser cuckoo *C. rochii* (64 g). It is especially interesting that *C. rochii* exploits dome-nesting hosts in Madagascar, the only region in which there is no overlap between *Cuculus* and *Chrysococcyx*. Even so, these two *Cuculus* species are much larger than is the largest *Chrysococcyx* cuckoo (38 g) and it is unlikely that they can enter the host nest. Instead, they probably squirt their eggs through the entrance hole, as the common cuckoo, *C. canorus*, does when laying in the domed nest of the wren, *Troglodytes troglodytes* (Dunn, 1985).

We found that *Chrysococcyx* cuckoos lay eggs more similar in size to their host eggs than do *Cuculus* cuckoos (Figure 5). Our analysis suggests this is probably a consequence of the fact that *Chrysococcyx* cuckoos are a closer match in body size to their hosts than are *Cuculus* cuckoos (Figure 4a,b), because *Chrysococcyx* cuckoos do not lay proportionally smaller eggs in relation to their body size (Figure 7). Selection has probably favored a smaller body size in *Chrysococcyx* cuckoos to enable them to enter their hosts' domed nests. Nevertheless, without a detailed analysis of cuckoo body size in relation to host nest entrance hole size, we cannot conclude that this is the only explanation. In addition, the incubation hypothesis could also help to explain differences from *Cuculus* cuckoos. *Chrysococcyx* cuckoos might not need to lay larger eggs than those of the host, because their young do not face the same time pressure to eject host eggs as *Cuculus* cuckoos do. The longer incubation times in dome-nesting hosts might have made this constraint on egg size weaker.

A third hypothesis could also apply; if dome-nesting hosts have more refined egg size discrimination, then the closer match in body size between *Chrysococcyx* and their hosts may have evolved to enable these cuckoos to lay an egg more similar in size to the host egg. Although no *Chrysococcyx* hosts have yet been tested for size discrimination, two other dome-nesting hosts of brood parasites are known to discriminate strongly against foreign eggs that are slightly larger than their own eggs (Marchetti, 2000; Mason and Rothstein, 1986). By contrast, although hosts of *C. canorus* discriminate against eggs very much larger than their own, they accept a cuckoo's egg a little larger than their own, provided it is a good match in color and spotting (Davies and Brooke, 1988, 1989). Perhaps dome-nesters rely more on size as a cue to discriminate foreign eggs because they cannot see color and spotting patterns so well in their dark nests. Open nesters, by contrast, may rely more on visual cues. It is even possible that a cuckoo egg slightly larger than the host egg has been favored for open cup–nesting hosts to increase its attractiveness, perhaps to compensate for any deficiencies in color and pattern mimicry (Alvarez, 1999, 2000; Baerends and Drent, 1982). Further experiments are needed to test these ideas.

APPENDIX

Raw data for the 136 cuckoo species used in the analyses

Species	BS	BW	EV	PH	HE	HB
Clamator jacobinus serratus	Ne	72.0	6.66	2.20	2.81	32.8
Clamator jacobinus jacobinus	Ne	66.0	4.42	1.11	3.99	59.5
Clamator levaillantii	Ne	124.0	5.85	1.69	4.34	73.4
Clamator coromandus	Ne	77.0	7.28	0.99	5.71	77.5
Clamator glandarius	Ne	124.0	9.69	0.36	16.19	345.5
Pachycoccyx audeberti	E	115.0	3.54	4.10		28.0
Cuculus crassirostris						
Cuculus sparverioides	E	150.0	4.97	2.77	4.02	54.1
Cuculus varius	E	104.0	5.51	1.45	5.15	71.8
Cuculus vagans		56.0				
Cuculus fugax	E	83.0	4.30	5.89	2.09	14.1
Cuculus pectoralis		80.0				
Cuculus solitarius	E	75.0	3.64	2.83	3.12	26.5
Cuculus clamosus	E	85.0	4.60	1.71	3.76	49.8
Cuculus micropterus	E	119.0	4.60	2.72	4.49	43.7
Cuculus canorus	E	115.0	3.39	7.19	1.87	16
Cuculus gularis	E	110.0	4.13	1.53	4.07	72
Cuculus saturatus	E	90.6	2.74	11.05	1.22	8.2
Cuculus horsfieldi	E	99.0	2.77	7.12	1.25	13.9
Cuculus poliocephalus	E	52.0	2.74	3.35	2.43	15.5
Cuculus rochii	E	64.0	1.80	7.80	1.03	8.2
Cuculus pallidus	E	82.0	3.26	3.42	3.19	24
Cercococcyx mechowi	E	55.0	3.39	5.73	2.145	9.6
Cercococcyx olivinus	E	65.0	3.15	6.50	3.017	10
Cercococcyx montanus	E	54.0	2.41	2.98	2.329	18.1
Cacomantis sonneratii	E	37.0	1.80	3.63	2.332	10.2
Cacomantis merulinus	E	23.5	1.32	3.09	1.077	7.6
Cacomantis variolosus	E	34.0	1.90	2.76	1.969	12.3
Cacomantis heinrichi						
Cacomantis castaneiventris	E	34.0	1.90	3.91	2.696	8.7
Cacomantis flabelliformis	E	44.0	2.41	3.83	1.77	11.5
Chrysococcyx osculans	E	30.0	1.99	2.31	2.2	13
Chrysococcyx basalis	E	22.0	1.32	2.44	1.26	9
Chrysococcyx minutillus	E	17.0	1.95	2.50	1.39	6.8
Chrysococcyx lucidus	E	23.0	1.32	2.80	1.27	8.2
Chrysococcyx ruficollis		23.5				
Chrysococcyx meyeri		20.0				
Chrysococcyx maculatus	E	24.0	1.25	2.67	1.72	9
Chrysococcyx xanthorhynchus	E	21.0	1.47	2.33	1.47	9

APPENDIX, continued

Species	BS	BW	EV	PH	HE	HB
Chrysococcyx flavigularis		30.0				
Chrysococcyx klaas	E	26.0	1.64	2.60	1.55	10
Chrysococcyx cupreus	E	38.0	2.30	1.86	1.55	20.4
Chrysococcyx caprius	E	32.0	2.41	1.21	2.02	26.5
Rhamphomantis megarhynchus		31.0				
Surniculus lugubris	E	35.0	2.45	1.69	1.871	20.7
Surniculus velutinus		36.0				
Caliechthrus leucolophus		117.0				
Microdynamis parva		43.0				
Eudynamys scolopacea	Ne	260.0	10.87	0.65	15.49	400
Eudynamys sco. cyanocephala	E	234.0	9.99	1.75	7.277	130
Eudynamys taitensis	E	120.0	3.46	6.67		
Scythrops novaehollandiae	Ne	613.0	21.11	1.28	18.35	480
Ceuthmochares aereus	P	66.0	8.09			
Phaenicophaeus diardi	P	57.0	9.18			
Phaenicophaeus sumatranus	P	114.0	8.08			
Phaenicophaeus tristis	P	115.0	11.72			
Phaenicophaeus viridirostris	P	77.0	9.24			
Phaenicophaeus leschenaultii	P	174.0	12.41			
Phaenicophaeus chlorophaeus	P	52.5	10.52			
Phaenicophaeus javanicus	P	98.0	7.82			
Phaenicophaeus calyorhynchus	P					
Phaenicophaeus curvirostris	P	122.0	15.59			
Phaenicophaeus pyrrhocephalus	P					
Phaenicophaeus superciliosus	P	117.5	8.81			
Phaenicophaeus cumingi	P	173.5	12.18			
Carpococcyx viridis	P					
Carpococcyx radiatus	P					
Carpococcyx renauldi	P	400.0	25.94			
Coua delalandei	P					
Coua gigas	P	415.0	22.72			
Coua coquereli	P	135.0	10.68			
Coua serriana	P	298.0				
Coua reynaudii	P	145.5	14.39			
Coua cursor	P	118.0	9.17			
Coua ruficeps	P	190.0	13.99			
Coua cristata	P	136.0	12.54			
Coua verreauxi	P					
Coua caerulea	P	235.0	15.33			
Centropus celebensis	P					
Centropus unirufus	P	184.0				
Centropus melanops	P	213.5	15.87			
Centropus nigrorufus	P		19.11			
Centropus milo	P					
Centropus goliath	P					
Centropus violaceus	P	500.0	25.06			
Centropus menbeki	P	517.0	16.98			
Centropus ateralbus	P	336.0	22.77			
Centropus phasianinus	P	340.0	16.30			
Centropus spilopterus	P		13.38			
Centropus bernsteini	P	160.0	11.03			
Centropus chalybeus	P					
Centropus rectunguis	P	163.5	16.98			
Centropus steerii	P					
Centropus sinensis	P	252.0	13.27			
Centropus andamanensis	P	234.0	13.99			
Centropus viridis	P	165.0	7.42			
Centropus toulou	P	150.0	11.38			
Centropus grillii	P	125.5	9.11			
Centropus bengalensis	P	120.0	8.52			
Centropus chlororhynchus	P		13.01			
Centropus leucogaster	P	315.0	15.19			
Centropus anselli	P	230.0				
Centropus monachus	P	204.0	12.83			
Centropus cupreicaudus	P	285.5	13.10			
Centropus senegalensis	P	170.0	11.72			
Centropus superciliosus	P	170.0	11.89			
Coccyzus pumilus	P	36.0	5.1			
Coccyzus cinereus	P	45.0	4.69			
Coccyzus erythropthalmus	P	50.5	6.07			
Coccyzus americanus	P	63.0	8.09			

APPENDIX, continued

Species	BS	BW	EV	PH	HE	HB
Coccyzus euleri	P	61.0				
Coccyzus minor	P	64.0	8.36			
Coccyzus ferrugineus	P	70.0				
Coccyzus melacoryphus	P	50.0	8.09			
Coccyzus lansbergi	P	47.0	5.3			
Saurothera merlini	P	154.0	18.36			
Saurothera vieilloti	P	80.0	10.84			
Saurothera longirostris	P	104.0	11.79			
Saurothera vetula	P	95.0	9.55			
Hyetornis pluvialis	P	130.0	12.27			
Hyetornis rufigularis	P	128.0				
Piaya cayana	P	98.0	12.07			
Piaya melanogaster	P	102.0	8.09			
Coccycua minuta	P	40.0	4.65			
Crotophaga major	P	153.5	33.14			
Crotophaga ani	P	105.0	12.07			
Crotophaga sulcirostris	P	75.0	9.11			
Guira guira	P	141.5	14.79			
Tapera naevia	E	52.0	3.24	3.71	2.46	14.1
Dromococcyx phasianellus	E	80.0	3.13	5.33	3.02	15.0
Dromococcyx pavonicus	E	48.0	2.41	3.20	3.02	15.0
Morococcyx erythropygus	P	62.0	6.07			
Geococcyx californianus	P	305.0	17.9			
Geococcyx velox	P	178.0	12.07			
Neomorphus geoffroyi	P	345.0	20.89			
Neomorphus radiolosus	P					
Neomorphus rufipennis	P		19.60			
Neomorphus pucheranii	P					

Abbreviations are as follows: BS indicates breeding strategy (P, parental care; Ne, nonejector; E, ejector); BW, cuckoo body weight in grams; EV, cuckoo egg volume in milliliters; PH, parasite-host mass ratio; HE, host egg volume in milliliters; and HB, host body weight in grams. Genera names and the species sequence follow Payne (1997).

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