

The evolution of cuckoo parasitism: a comparative analysis

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Cuckoos (family Cuculidae) show the highest diversity of breeding strategies within one bird family (parental care, facultative and obligate brood parasites). We used independent contrasts from two phylogenies to examine how this variation was related to 13 ecological and life-history variables. The ancestral state was probably tropical, resident, forest cuckoos with parental care. The evolution of brood parasitism was correlated with a shift to more open habitats, a change in diet, increases in species breeding-range size and migration, and a decrease in egg size. Once parasitism had evolved, more elaborate parasitic strategies (more harmful to host fitness) were correlated with decreased egg size, a change in diet, increased breeding-range size and migration, a shortened breeding season and a decrease in local abundance. Establishing the most probable evolutionary pathways, using the method of Pagel, shows that changes in ecological variables (such as migration, range size and diet type) preceded the evolution of brood parasitism, which is likely to be a later adaptation to reduce the cost of reproduction. By contrast, brood parasitism evolved before changes in egg size occurred, indicating that egg size is an adaptive trait in host–parasite coevolution. Our results suggest that the evolution of cuckoo brood parasitism reflects selection from both ecological pressures and host defences.

Keywords: brood parasitism; cuckoo; independent contrasts; life-history evolution

1. INTRODUCTION

The 136 species of cuckoos in the family Cuculidae are remarkably diverse in their breeding strategies, to a degree perhaps unmatched among the world's bird families (Payne 1977, 1997). While 83 species raise young themselves, 53 are brood parasites that lay their eggs in the nests of other species, which act as hosts and raise the parasite's chicks. This variation in the degree of parental care has long puzzled biologists (e.g. Gilbert White's letter XXX to Daines Barrington; White 1789). Darwin (1859) was the first to propose that parasitic cuckoos evolved from parental cuckoos. The traditional taxonomy of the cuckoo family supports this view and suggests that parasitism evolved independently in the two parasitic subfamilies, namely the Old World Cuculinae and the New World Neomorphae (Payne 1997). However, the phylogeny described by Hughes (2000), based on osteological characters, places New and Old World parasitic cuckoos together and suggests that brood parasitism evolved just once in the family, with the New World genus *Coccyzus* re-evolving parental care from a parasitic ancestor. By contrast, the molecular phylogeny reported by Aragon *et al.* (1999) suggests three independent origins of brood parasitism, namely in *Clamator*, other Old World cuckoos and New World cuckoos.

There is no clear consensus about what evolutionary forces have shaped this variety of breeding strategies (Rothstein & Robinson 1998; Davies 2000; Robert & Sorci 2001). On current evidence, the turacos, an entirely Afrotropical group, might be the closest living relatives of cuckoos (del Hoyo *et al.* 1997). Most turaco species live in forests, are sedentary and mainly frugivores. The basal

nodes of the cuckoo phylogenies described by both Hughes (2000) and Aragon *et al.* (1999) involve taxa with parental care that are also resident, tropical, forest dwellers, so these are the probable ancestral cuckoo traits. By contrast, parasitic cuckoos occupy a wide range of tropical and temperate habitats and many undergo long migrations. We therefore predict that the evolution of brood parasitism involved, especially, changes in habitat, migration, range size and diet.

Recent experimental studies have shown that cuckoo parasitic adaptations (e.g. host egg mimicry) coevolve with host defences (Davies & Brooke 1989a,b; Moksnes *et al.* 1991; Soler *et al.* 1994, 1998). However, a broader, comparative analysis is needed to understand how life-history and ecological factors shape host–parasite coevolution. Here, we use the two recently published phylogenies for the cuckoo family (Aragon *et al.* 1999; Hughes 2000) to address two questions:

- (i) What were the changes in ecology and life history when cuckoos evolved brood parasitism from an ancestor with parental care and did these changes precede the evolution of brood parasitism, or were they consequences?
- (ii) Once parasitism had evolved, how were parasite breeding strategies (costs inflicted on the host fitness) shaped by ecological factors, cuckoo life histories and host defences?

We attempt to answer these questions using an analysis that controls for phylogeny by computing independent contrasts (Felsenstein 1985; Harvey & Pagel 1991). Then we investigate the temporal order of changes in variables using the method of Pagel (1994, 1999), which allows us to establish whether changes in ecological and life-history

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Table 1. Variables used in the analysis.
(Superscript letters refer to the data source given below.)

variable	description and coding
breeding strategy ^{a,b,c}	0 = parental care, 1 = intraspecific brood parasite, 2 = facultative interspecific brood parasite, 3.0 = obligate interspecific brood parasite, host chicks often survive, no egg mimicry, 3.1 = 3.0, but egg with mimicry; 3.2 = 3.1 + mafia tactics; 3.3 = 3.1, but no host chicks survive (egg/chick eviction or killing)
body weight ^a	body weight in g
body size ^a	body length (tip of bill to tip of tail feathers) in cm
egg size ^a	egg length in mm
sexual plumage dimorphism ^a	0 = no difference, 1 = slight difference (eye colour or eye ring), 2 = difference (less than 25% of the plumage), 3 = marked difference (more than 25% of the plumage), 4 = different plumage
parasite–host ratio ^{a,d}	body mass of parasite divided by body mass of host (average if many)
specialization degree (interspecific parasite) ^{a,b,c}	1 = more than 30 host species, 2 = 11–30 host species, 3 = 6–10 host species, 4 = 1–5 host species
diet ^a	1 = seeds, 2 = fruits, 3 = insects, 4 = snails, 5 = frogs, 6 = small lizards, 7 = larger reptiles, 8 = birds, 9 = mammals
habitat ^a	0 = open grassland, semi-desert, 1 = wooded savannahs, 2 = temperate and subtropical forests, 3 = closed tropical rainforests
habitat productivity ^c	productivity in g carbon m ⁻² per annum of the breeding region
season length ^a	length of the breeding season in months
migration pattern ^a	0 = resident, 1 = rare migrant (vacates less than 25% of breeding area), 2 = partial migrant (vacates 25–75% of breeding area), 3 = migrant (vacates more than 75% of breeding area), 4 = long distance seasonal migrant (vacates 100% of breeding area and migrates commonly more than 5000 km)
breeding range size ^{a,f}	range size estimate in log km ²
population status ^a	0 = extinct, 1 = endangered, 2 = vulnerable, 3 = rare, 4 = scarce, 5 = uncommon, 6 = common, 7 = fairly common, 8 = very common, 9 = abundant

^a Payne (1997).

^b Brooker & Brooker (1989).

^c Rowan (1983).

^d Dunning (1993).

^e Reichle (1970).

^f BirdLife International (2000).

variables preceded the evolution of brood parasitism or were consequences of it.

2. METHODS

We compiled, from the literature, data on 14 variables (table 1) for the 136 species in the family Cuculidae (Rowan 1983; Brooker & Brooker 1989; Payne 1997; Davies 2000). A summary is given in electronic Appendix A available on The Royal Society's Publications Web Site. Two species (*Oxylophus jacobinus* and *Eudynamis scolopacea*) were entered twice since they have two clearly defined subspecies, which differ in many variables. For cuckoo species using several breeding strategies, we took the maximum value according to our rank scheme. For genus-level analysis we used mean values for the species in the genus. Breeding strategies were ranked according to the cost they impose on host fitness, because we assumed that more costly parasitic strategies (egg mimicry, host-egg ejection) evolved from less costly ones (no egg mimicry, no host-egg ejection). We ranked the different interspecific brood parasitism strategies as variants of the general strategy obligate brood parasite (hence, 3.1 to 3.3 and not 4 to 6, see breeding strategy variable in table 1). This allows for a more conservative interpretation of our results. Host body weights were obtained from Dunning (1993) and habitat productivity data were taken from Reichle (1970). The ranking of diet types reflects

nutritional value and especially prey size. Range sizes were calculated by overlaying distribution maps with world country maps. For species with a small range, we used large-scale maps or the information in BirdLife International (2000). The population status categories were taken from Payne (1997) and refer to local abundance within the breeding range. In analyses involving non-parasitic taxa, we omitted the variables parasite–host mass ratio and host specialization since they cannot be scored for non-parasitic taxa. To calculate means for genera for the independent contrast analyses, we treated categorical variables essentially as continuous, since the categories reflect a rather continuous spectrum of diet type, migration, pattern etc.

At the start, we have included a cross-species analysis because it not only provides additional insight into the current status of an adaptive radiation (Price 1997), but also recent evidence suggests that sometimes a cross-species analysis is statistically more sound than an independent contrast approach (Harvey & Rabaut 2000). However, in this case it is clear that there is an extensive bias due to a few speciose genera (e.g. *Cuculus*, *Chrysococcyx*) that share similar traits.

The phylogenetically controlled comparative analysis was based on Felsenstein's (1985) method of independent contrasts. We used two different phylogenetic trees: the tree described by Hughes (2000) is based on osteological characters and uses genera as the level of comparison, whereas Aragon *et al.* (1999) compared species using cytochrome *b* sequence data. The two

phylogenetic trees differ mainly in that Hughes (2000) found evidence for a monophyletic origin of all brood parasitic cuckoos, whereas Aragon *et al.* (1999) described three independent evolutions of brood parasitism. With 35 (two genera, *Cercococcyx* and *Scythrops*, were included based on information in Payne (1997)) and 20 taxonomic levels, respectively, 34 and 19 contrasts could be computed. We also used CAIC (Purvis & Rambaut 1995), which produced similar results, but preferred to use Felsenstein's contrasts because CAIC makes all contrasts in the dependent variable positive and hence, in our case, produces a highly skewed and non-normal distribution. To exclude the possibility that spurious correlations arise from zeros in the breeding strategy contrasts, we used the BRUNCH algorithm in CAIC to calculate contrasts only when changes occurred in breeding strategy.

Contrasts were standardized using their variance as recommended by Felsenstein (1985) and there were no correlations between contrasts in breeding strategy and their standard deviation ($r_{32} = 0.262$, $p = 0.134$ for Hughes's tree and $r_{17} = 0.198$, $p = 0.414$ for Aragon's tree), which ensures that all contrasts are weighted equally in the dataset (Garland *et al.* 1992; Krüger 2000). Stepwise forward multiple regression analysis through the origin was performed on the contrasts, as recommended by Harvey & Pagel (1991). We looked at tolerance levels to check for redundancy among our explanatory variables and used a threshold of 0.1 to indicate an independent effect, as recommended in Hair *et al.* (1995). Residuals of all models were checked for normality and the importance of predictor variables was not ranked (James & McCulloch 1990).

In order to establish the most likely evolutionary pathway between two traits, we used Pagel's discrete variable method (Pagel 1994, 1999). This method uses a continuous-time Markov model to describe evolutionary changes along each branch of a phylogenetic tree. This allows us to test the temporal ordering and direction of evolutionary change and establishes the most probable evolutionary pathway between two variables (Rolland *et al.* 1998, Cezilly *et al.* 2000). Hence this allows us to disentangle cause and effect of a correlation between two traits. As variables need to be dichotomous for this method, we used the mean of the data as a threshold. (For a detailed description of the model and the tests, see Pagel (1994, 1999).) As the method can only look at one variable pair at a time, controlling for additional variables is not possible. The full dependent model tests for correlated evolution between two variables. It is referred to as the full model because none of the eight possible transition parameters (see figure 1) is set to zero.

3. RESULTS

(a) Comparisons across species and genera

Across all species of the Cuculidae, there were significant differences between species with parental care (table 1; breeding strategy 0–2) and obligate interspecific brood parasites (breeding strategy 3.0–3.3) in all but two variables (table 2). Interspecific brood parasites are of lower mass, are smaller, lay smaller eggs, have a higher plumage dimorphism and eat smaller prey. They live in more open, less productive habitats, are more migratory and have a larger breeding-range size. To test whether these results are biased by speciose genera, we compared genera means. Parasitic genera are smaller, lay smaller eggs, eat smaller prey, are more migratory and have larger breeding ranges (table 2). Combining species into genera indicates the

need for phylogenetic correction because many of the significant differences across species disappeared in the cross-genera analysis.

(b) Independent contrast analysis

Considering all cuckoo genera (parental and parasitic), the independent contrast analysis based on the tree of Hughes (2000) resulted in a regression model that explained 36% of the variation in breeding-strategy contrasts with four variables (table 3a). As in both the cross-species and genera analyses, migration and range size were significant predictors; the evolution of more parasitic breeding strategies was correlated with an increase in breeding range size and migration. More parasitic breeding strategies were also correlated with occupancy of more open habitat and a decrease in population status. Results changed little if only non-zero breeding strategy contrasts were included (table 3b) but the model gained considerably in explanatory power (65% of the variation in breeding strategy explained). As in the full model, habitat, range size and migration were significant predictors, habitat productivity was a new predictor and replaced population status.

When only parasitic genera were used in the analysis (i.e. breeding strategy 1–3.3 in table 1), four variables together explained 68% of the variation in parasitism strategy contrasts (table 3c). The evolution of more parasitic strategies was correlated with increased migration, increased breeding-range size, decreased breeding-season length and decreased egg size. Migration pattern and range size were also significant predictors in the analysis involving all genera, as was egg size in the cross-species analysis.

Basing the analysis of both parental and parasitic cuckoos on the different phylogenetic tree of Aragon *et al.* (1999) produced a regression model that explained 82% of the variation in breeding-strategy contrasts with four variables (table 4a). As in the contrast analysis based on the phylogenetic tree described by Hughes (2000), evolution of increased parasitism correlated with increased migration and increased breeding-range size. Two new variables entered the model with a negative coefficient: increased parasitism correlated with smaller eggs and a diet with smaller prey items. Egg size was also a significant predictor in both the cross-species and genera analyses (table 2). Omitting the non-zero breeding-strategy contrasts changed the model very little (table 4b). Diet, egg size and migration were significant predictors and the model explained 81% of the variation in breeding strategy.

For contrasts involving only parasitic species in the phylogeny described by Aragon *et al.* (1999) (table 4c), three variables together explained 88% of the variation: more costly (to host fitness) parasitism strategies correlated with decreased egg size, decreased population status and smaller prey items. Of these, only egg size was a significant predictor in the analysis using parasitic contrasts based on the phylogenetic tree described by Hughes (2000).

(c) Evolutionary pathways

We looked finally at the most probable evolutionary pathways between breeding strategy and important predictor variables of the contrast analyses. Two variables that were important in all three analyses based on the phylogeny reported by Hughes (2000) were migration pattern

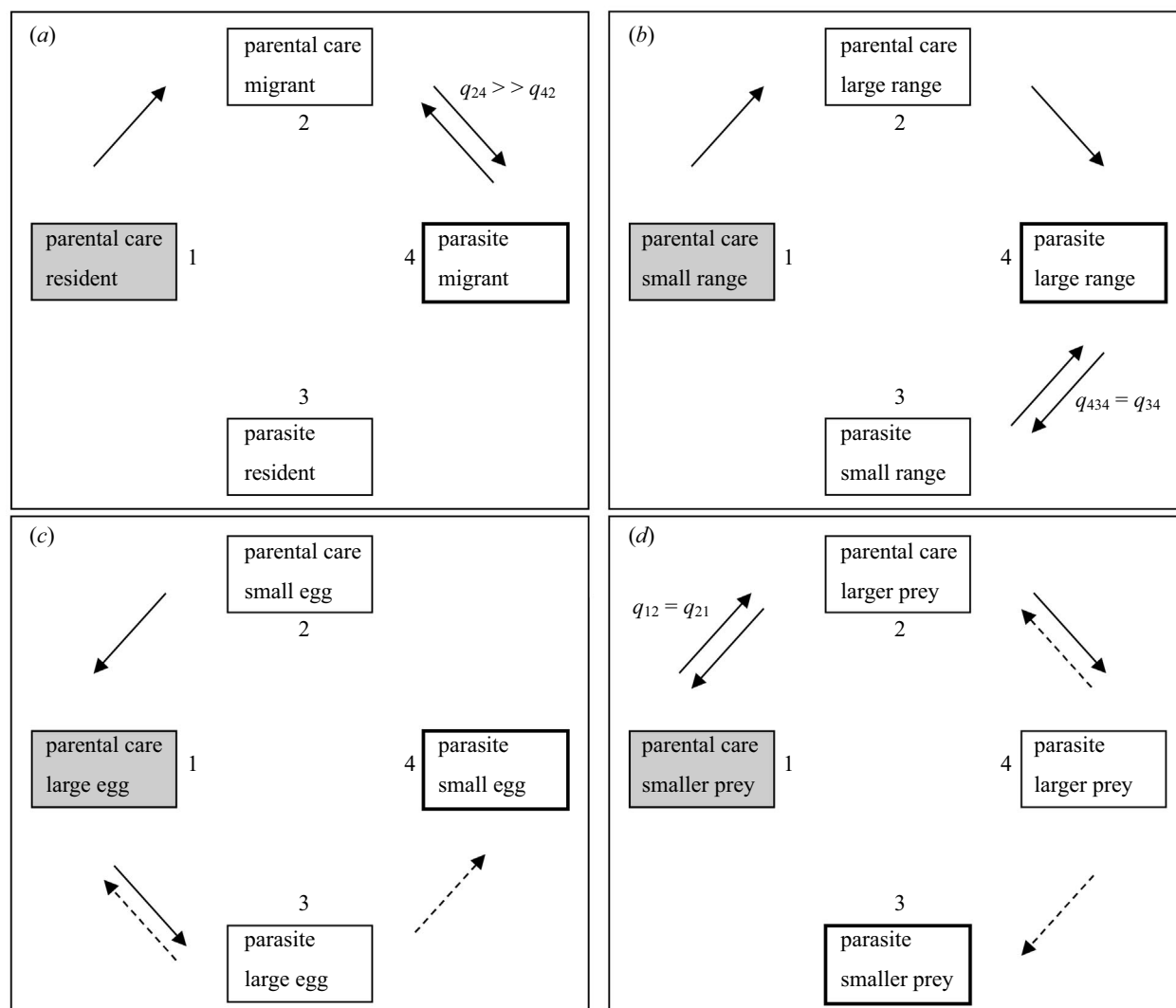


Figure 1. Flow diagram of the most probable evolutionary pathways between breeding strategy and (a) migration pattern and (b) breeding range size, based on the phylogeny described by Hughes (2000); and between breeding strategy and (c) egg size and (d) diet type, based on the phylogeny described by Aragon *et al.* (1999). In each figure part, the presumed ancestral state is shaded in light grey, whereas the common current state in parasitic cuckoos is the boldly lined box. Solid arrows represent significant evolutionary pathways ($p < 0.05$) and dashed lines represent trends ($p < 0.1$). A comparison of transition rates (q) is given when both transition rates were significant, with subscripts indicating the transition directions.

and breeding-range size, and the corresponding two variables from analyses based on the phylogeny reported by Aragon *et al.* (1999) were egg size and diet.

The flow diagrams of the most likely evolutionary pathways are presented in figure 1. With regard to breeding strategy and migration (figure 1a), the full dependent model had a log-likelihood value of -22.831 . The only significant pathway leads via changes in migration occurring first (log likelihood = -24.861 , likelihood ratio = 4.060 , $p < 0.05$), before the evolution of brood parasitism (log likelihood = -24.813 , likelihood ratio = 3.964 , $p < 0.05$). A migrating parasitic species can re-evolve parental care (log likelihood = -24.803 , likelihood ratio = 3.944 , $p < 0.05$).

With regard to breeding strategy and breeding range size (figure 1b), the full dependent model had a log likelihood value of -29.971 . The transition from parental care and a small breeding range towards a parasite with a large breeding range can only take place via changes in breeding-range size (log likelihood = -32.411 , likelihood

ratio = 4.880 , $p < 0.05$) preceding changes in breeding strategy (log likelihood = -32.106 , likelihood ratio = 4.270 , $p < 0.05$). There is no significant pathway from parental care with a small breeding range to parasitic with a small breeding range. A parasite with a large breeding range can subsequently re-evolve a small range (log likelihood = -34.693 , likelihood ratio = 9.444 , $p < 0.005$) and vice versa (log likelihood = -32.396 , likelihood ratio = 4.850 , $p < 0.05$).

With regard to breeding strategy and egg size (figure 1c), the full dependent model had a log-likelihood value of -15.370 . The most probable pathway from the ancestral state (parental care with a large egg) is first the evolution of brood parasitism (log likelihood = -17.430 , likelihood ratio = 4.120 , $p < 0.05$), followed by a decrease in egg size (log likelihood = -16.879 , likelihood ratio = 3.018 , $p < 0.1$). A parasitic cuckoo with a large egg size can re-evolve parental care (log likelihood = -16.926 , likelihood ratio = 3.112 , $p < 0.1$) and there is also a significant transition from parental care with a small egg

Table 2. Comparing variable means (s.d. in parentheses) between species or genera with parental care and obligate interspecific brood parasites.

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Note: sample sizes vary because not all variables were known for every species.

variable	species comparison		genera comparison	
	with parental care	interspecific brood parasites	with parental care	interspecific brood parasites
<i>n</i>	53–83	47–53	19	17
body weight	168.3 (111.0)	80.7 (87.6)***	147.4 (99.6)	103.5 (131.6)
body size	44.2 (10.3)	28.9 (9.3)***	41.4 (9.5)	30.5 (10.7)**
egg size	34.5 (5.0)	24.1 (6.0)***	33.9 (5.0)	24.7 (7.2)***
plumage dimorphism	0.1 (0.4)	0.9 (1.3)***	0.2 (0.7)	0.8 (1.3)
diet	4.1 (1.5)	3.1 (0.8)***	3.9 (1.0)	3.1 (1.0)*
habitat	2.5 (0.7)	2.2 (0.7)*	2.5 (0.7)	2.2 (0.6)
habitat productivity	639.2 (130.5)	568.2 (164.8)**	647.2 (125.0)	601.2 (133.9)
season length	4.4 (1.9)	4.0 (1.5)	3.8 (1.3)	4.4 (1.6)
migration pattern	0.1 (0.3)	1.4 (1.4)***	0.1 (0.3)	1.1 (1.3)***
breeding-range size	5.6 (1.2)	6.5 (0.7)***	5.8 (0.8)	6.4 (0.6)**
population status	4.9 (1.9)	5.5 (1.2)	5.4 (1.4)	5.4 (1.1)

towards parental care with a large egg (log likelihood = -18.869 , likelihood ratio = 6.998 , $p < 0.02$).

Finally, the flow diagram for breeding strategy and diet type (figure 1d) indicates that changes in diet type preceded changes in breeding strategy. The full dependent model had a log-likelihood value of -21.161 . Although the evolution of brood parasitism and small prey from the ancestral state of parental care and small prey would involve one transition only, the most likely evolutionary pathway seems to be that first diet changed to larger prey (log likelihood = -23.864 , likelihood ratio = 5.406 , $p < 0.02$), then brood parasitism evolved (log likelihood = -23.866 , likelihood ratio = 5.410 , $p < 0.02$) and finally prey became smaller again (log likelihood = -22.836 , likelihood ratio = 3.350 , $p < 0.1$). In addition, a cuckoo with parental care and feeding on large prey can re-evolve feeding on smaller prey (log likelihood = -24.114 , likelihood ratio = 5.906 , $p < 0.02$) and a parasitic cuckoo feeding on large prey can re-evolve parental care (log likelihood = -22.650 , likelihood ratio = 2.978 , $p < 0.1$).

4. DISCUSSION

Our study suggests that the evolution of cuckoo breeding strategies might be explained as a two-step process.

(a) From parental care to parasitism

The independent contrast analyses, excluding the zero contrasts in the breeding-strategy column, reveal which variables change significantly when there are evolutionary changes in breeding strategy (tables 3b and 4b). The analyses showed that the evolution of brood parasitism entailed significant increases in migration (both phylogenies), a shift to more open habitat and an increase in breeding-range size (phylogeny reported by Hughes (2000)) and decreased egg size and diet with smaller prey (phylogeny reported by Aragon *et al.* (1999)). How might we explain these changes?

The analysis of evolutionary pathways suggests that changes in ecology and life history preceded the evolution of brood parasitism, with the exception of egg size.

Assuming an ancestral state of tropical, resident, forest cuckoos with parental care, there was first an expansion to colonize more open and seasonal habitats, resulting in more migration, an increased breeding-range size and a change in diet. These changes were then followed by the evolution of brood parasitism. This may be due to selection pressures on reducing the cost of reproduction (Payne (1974) estimated that a parasitic cuckoo needs only about half the energy to achieve the same reproductive success as a parental cuckoo). The most probable scenario based on our results, therefore, is that the evolution of brood parasitism is a consequence, not a cause, of changes in ecology.

Once brood parasitism had evolved, cuckoo egg size became smaller (figure 1c). Two hypotheses could explain this. First, freed from parental duties, parasitic cuckoos could increase their clutch size (Payne 1974) and a decrease in egg size may have facilitated this. Second, smaller eggs may have evolved in response to host defences (see below).

(b) The evolution of more elaborate parasitic strategies

The independent contrast analyses showed that increasingly costly parasitism to hosts was correlated with the following: decreased egg size (both phylogenies), increased migration and breeding-range size and decreased breeding-season length (Hughes (2000) phylogeny), and smaller prey items and a decreased local population abundance (phylogeny reported by Aragon *et al.* (1999)).

Some of these changes may reflect parasite–host coevolution. The relatively smaller eggs of parasitic cuckoos has been noted before (Payne 1974) and is likely to reflect the fact that most parasitic cuckoos exploit hosts that are smaller than themselves. On average, smaller species are more abundant than larger species (Brown 1995), so the exploitation of small hosts will increase egg-laying opportunities (Payne 1974). It may also be easier for a parasite to withstand attacks from smaller hosts when it approaches host nests. Once small hosts are favoured, a decrease in cuckoo egg size will be selected for, both to increase host acceptance of the parasitic egg (Davies

Table 3. Independent contrasts analysis based on the phylogeny described by Hughes (2000).

((a) Analysis of all contrasts ($n = 34$). The model is highly significant ($F_{4,30} = 4.259$, $p = 0.008$) and residuals are normal (s.e. of the estimate: 0.306). (b) Analysis excluding all zero contrasts from the breeding-strategy column ($n = 17$). The model is highly significant ($F_{4,13} = 6.138$, $p = 0.005$) and residuals are normal (s.e. of the estimate: 0.342). (c) Analysis of contrasts among parasitic (facultative and obligate) taxa only ($n = 18$). The model is significant ($F_{4,13} = 3.824$, $p = 0.031$) and residuals are normal (s.e. of the estimate: 0.299).)

(a) analysis of all contrasts

variable	β	s.e.	t (d.f.)	p	r^2	tolerance
habitat	-0.335	0.154	2.174 (33)	0.038	0.124	0.500
migration pattern	0.267	0.101	2.652 (32)	0.013	0.268	0.958
breeding range size	0.335	0.137	2.445 (31)	0.021	0.324	0.865
population status	-0.220	0.095	2.328 (30)	0.027	0.362	0.461

(b) analysis excluding all zero contrasts from the breeding strategy column

variable	β	s.e.	t (d.f.)	p	r^2	tolerance
habitat	-0.754	0.330	2.289 (16)	0.039	0.296	0.823
breeding range size	0.768	0.249	3.084 (15)	0.009	0.383	0.723
migration pattern	0.682	0.216	3.161 (14)	0.008	0.531	0.343
habitat productivity	-0.004	0.002	2.157 (13)	0.047	0.654	0.340

(c) analysis of contrasts among parasitic (facultative and obligate) taxa only

variable	β	s.e.	t (d.f.)	p	r^2	tolerance
migration pattern	0.224	0.102	2.196 (17)	0.045	0.280	0.916
breeding range size	0.653	0.236	2.766 (16)	0.017	0.396	0.751
season length	-0.107	0.045	2.378 (15)	0.035	0.531	0.884
egg size	-0.036	0.016	2.251 (14)	0.042	0.682	0.827

Table 4. Independent contrasts analysis based on the phylogeny described by Aragon *et al.* (1999).

((a) Analysis of all contrasts ($n = 19$). The model is highly significant ($F_{4,15} = 17.131$, $p < 0.001$) and residuals are normal (s.e. of the estimate: 0.305). (b) Analysis excluding all zero contrasts from the breeding strategy column ($n = 14$). The model is highly significant ($F_{3,11} = 15.989$, $p < 0.001$) and residuals are normal (s.e. of the estimate: 0.363). (c) Analysis of contrasts among parasitic (facultative and obligate) taxa only ($n = 10$). The model is highly significant ($F_{3,7} = 17.743$, $p = 0.001$) and residuals are normal (s.e. of the estimate: 0.205).)

(a) analysis of all contrasts

variable	β	s.e.	t (d.f.)	p	r^2	tolerance
egg size	-0.101	0.026	3.847 (18)	0.002	0.449	0.845
migration pattern	0.495	0.212	2.339 (17)	0.034	0.649	0.729
breeding range size	0.368	0.098	3.761 (16)	0.002	0.747	0.687
diet type	-0.378	0.153	2.472 (15)	0.026	0.820	0.511

(b) analysis excluding all zero contrasts from the breeding strategy column

variable	β	s.e.	t (d.f.)	p	r^2	tolerance
diet type	-0.758	0.304	2.493 (13)	0.030	0.610	0.592
egg size	-0.089	0.033	2.710 (12)	0.020	0.746	0.787
migration pattern	0.605	0.284	2.130 (11)	0.048	0.813	0.682

(c) analysis of contrasts among parasitic (facultative and obligate) taxa only

variable	β	s.e.	t (d.f.)	p	r^2	tolerance
egg size	-0.053	0.016	3.285 (9)	0.017	0.576	0.648
population status	-0.357	0.056	6.411 (8)	0.001	0.708	0.750
diet type	-0.340	0.092	3.695 (7)	0.010	0.884	0.623

& Brooke 1988; Marchetti 2000) and to improve its incubation efficiency (Payne 1974; Davies & Brooke 1988).

There may have been an interplay between ecological and host selection pressures. For example, the move to more open, less productive habitats is likely not only to

have favoured the evolution of brood parasitism in the first place, but also more refined parasitic strategies to further reduce the cost of reproduction.

With regard to diet, many parasitic cuckoos live in forests, where they feed on insects, especially caterpillars

(Payne 1997). In contrast to parental species, however, their choice of breeding habitat will not be limited by the need for a suitable food supply. Parasitic cuckoos can rely on the parental care of host species adapted to a variety of habitats, including habitats where cuckoos themselves cannot feed. For example, common cuckoos *Cuculus canorus* often commute long distances (5–20 km) between host breeding areas in marshland and moorland and their feeding areas in woodland (Wyllie 1981; Dröscher 1988; Nakamura & Miyazawa 1997). This freedom from laying eggs close to feeding sites and the exploitation of host species with a variety of ecological adaptations might have further increased the breeding-range size of parasitic cuckoos.

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