Behavioral Ecology
doi:10.1093/beheco/ari041
Advance Access publication 13 April 2005

The evolution of egg rejection by cuckoo hosts in Australia and Europe

N.E. Langmore,[a] R.M. Kilner,[b] S.H.M. Butchart,[b] G. Maurer,[a] N.B. Davies,[b] A. Cockburn,[a] N.A. Macgregor,[a,b] A. Peters,[a,c] M.J.L. Magrath,[d] and D.K. Dowling[d]
[a]School of Botany & Zoology, Australian National University, ACT, 0200, Australia, [b]Department of Zoology, University of Cambridge, Downing Street, CB2 3EJ, UK, [c]Max Planck Research Centre for Ornithology, P.O. Box 1564, D-82305 Starnberg (Seewiesen), Germany, and [d]Department of Zoology, University of Melbourne, Victoria 3010, Australia

Exploitation of hosts by brood parasitic cuckoos is expected to stimulate a coevolutionary arms race of adaptations and counteradaptations. However, some hosts have not evolved defenses against parasitism. One hypothesis to explain a lack of host defenses is that the life-history strategies of some hosts reduce the cost of parasitism to the extent that accepting parasitic eggs in the nest is evolutionarily stable. Under this hypothesis, it pays hosts to accept cuckoo eggs if (1) the energetic cost of raising the cuckoo is low, (2) there is time to renest, and (3) clutch size is small. We parasitized the nests of host and nonhost species with nonmimetic model eggs to test whether the evolution of egg recognition by cuckoo hosts could be explained by life-history variables of the host. The most significant factor explaining rates of rejection of model eggs was whether or not a species was a cuckoo host, with hosts rejecting model eggs at a higher rate than nonhosts. Egg-rejection rates were also explained by visibility within the nest and by cuckoo mass. We found little support for the life-history model of egg rejection. Our results suggest that parasitism is always sufficiently costly to select for host defenses and that the evolution of defenses may be limited by proximate constraints such as visibility within the nest. *Key words:* brood parasitism, coevolution, cowbirds, cuckoos, life-history strategies. *[Behav Ecol 16:686–692 (2005)]*

Interactions between cuckoos and their hosts have long been presented as a model example of coevolution (Davies and Brooke, 1988; Dawkins and Krebs, 1979; Rothstein, 1990, Rothstein and Robinson, 1998). Brood parasitism is costly for hosts because hosts waste time and energy nurturing cuckoo nestlings that have evicted their own offspring from the nest. The high cost of parasitism sets in motion a coevolutionary arms race between cuckoos and their hosts. As hosts evolve defenses against parasitism by cuckoos, cuckoos evolve ever better means of tricking hosts into rearing their young, which, in turn, promotes the evolution of improved host defenses. Hosts can resist parasitism by mobbing adult cuckoos near the nest (e.g., Duckworth, 1991; Moksnes et al., 1991), rejecting any odd eggs that appear in their nest (e.g., Davies and Brooke, 1989a), deserting parasitized clutches (e.g., Hosoi and Rothstein, 2000), and by deserting cuckoo chicks (Langmore et al., 2003). Cuckoos have retaliated by laying their eggs very rapidly and at times when hosts are unlikely to be near the nest, by evolving egg color patterns that match those of their hosts, and by producing young that mimic host offspring (Brooke and Davies, 1988; Chance, 1940; Davies and Brooke, 1989a,b; Higuchi, 1998; Langmore et al., 2003).

However, some hosts seem to lack defenses against parasitism because they fail to reject odd-looking eggs that are added to their nests (e.g., dunnocks *Prunella modularis*, Brooke and Davies, 1988; splendid fairy-wrens *Malurus splendens*, Brooker and Brooker, 1996). One explanation is that these hosts accept parasites in their nest because they have not yet had time to evolve resistance to cuckoos (Davies and Brooke, 1989b).

Alternatively, evolutionary equilibrium models consider the balance of the costs and benefits accrued by rejecting odd eggs from the nest. One type of model argues that acceptance of cuckoo eggs in the nest may be the best option if the cost of resisting parasitism outweighs the benefits to be gained (e.g., Lotem and Nakamura, 1998; Takasu et al., 1993). For example, when mimicry of host eggs by brood parasites is very accurate, hosts may make recognition errors and reject their own eggs at such a high rate that it becomes more beneficial to accept all eggs than to attempt discrimination of cuckoo eggs (Davies et al., 1996).

A different evolutionary equilibrium model, the life-history hypothesis, argues that parasitism by cuckoos may be cost free at the population level, so host defenses can bring no benefit. Some hosts may have life-history strategies that reduce the cost of parasitism to the extent that accepting parasitic eggs in the nest is evolutionarily stable (Brooker and Brooker, 1996). Specifically, it may pay hosts to accept cuckoo eggs if (1) the energetic cost of raising the cuckoo is low, (2) there is time to renest, and (3) clutch size is small. According to this hypothesis, host reproductive success is not reduced by rearing a cuckoo, and therefore hosts are unlikely to evolve defenses against parasitism.

The majority of studies of cuckoos and their hosts have been performed in the northern hemisphere, where clutch sizes are often relatively large and breeding seasons are short. However, the conditions that are likely to favor acceptance of cuckoo parasitism are more common in the southern hemisphere. For example, hosts of Australian cuckoos lay relatively small clutches, and they may renest repeatedly for six or more months. Furthermore, the small Australian hosts may experience far lower energetic costs when rearing a cuckoo than their European counterparts. These Australian birds are parasitized by bronze-cuckoos *Chalcites* spp., which are only twice their body weight, whereas all the small European hosts are parasitized by the European cuckoo *Cuculus canorus*, which may be up to 10 times their body mass.

Address correspondence to: N. Langmore. E-mail: naomi.langmore@anu.edu.au.

Received 21 August 2004; revised 8 February 2005; accepted 11 February 2005.

Brooker and Brooker (1996) conducted the first comparative test of their hypothesis using data from 4 Australian cuckoo hosts and 18 European cuckoo hosts. They found general support for their model: hosts were more likely to reject model eggs if they were migratory and had a short breeding season, if they had a large clutch size, and if they were parasitized by a relatively large species of cuckoo.

Soler (1999) subsequently retested the predictions of the model, this time using a comparative analysis that controlled for common phylogenetic descent. He analyzed the effects of life-history variables on rejection rates of hosts of the European cuckoo only and failed to find any support for the life-history hypothesis.

We incorporated ideas from both these studies in a new analysis of the influence of life-history variables on egg-rejection behavior. We considered the greatest deficiency in existing analyses to be data on rejection rates in Australian hosts. As explained above, Australian hosts are more likely to exhibit the life-history traits that are predicted to be associated with an "acceptor" strategy than European hosts, yet no studies have compared hosts within Australia that are likely to be "acceptors" with those that are likely to be "rejectors." We tested the egg-rejection behavior of 18 Australian cuckoo hosts and nonhosts with model eggs and combined the results with published data on 23 European host and nonhost species (taken from Davies and Brooke, 1989a, and Moksnes et al., 1991) exhibiting a range of life-history strategies to test this hypothesis. The use of phylogenetically based comparative analyses is contentious, and it has been recommended that the results of both phylogenetically based and nonphylogenetic analyses should be presented in comparative studies (Blackburn and Gaston, 1998; Price, 1997; Schluter, 2000). Therefore, we performed two analyses, one of which controlled for common phylogenetic descent. We predicted that if hosts are involved in a coevolutionary arms race with cuckoos, then they are more likely than nonhosts to have evolved the ability to recognize and reject a nonmimetic egg that is placed in their nest. By contrast, if hosts and cuckoos have reached an evolutionary equilibrium as predicted by the life-history model, then hosts should be less likely to reject odd eggs in their nests. Furthermore, we predicted that if the cost of parasitism is important in determining rejection rates, we should find higher rejection rates in species with larger clutches, a shorter breeding season, and those that are parasitized by a large cuckoo relative to their own body size.

METHODS

Egg-rejection experiments in Australia

Study sites

Model egg experiments were performed on a range of host and nonhost species in Australia between 1999 and 2002 (Table 1). "Hosts" are species that can successfully rear a cuckoo chick (accessible nest, suitable diet) and that are regularly or occasionally parasitized. "Nonhosts" are species that are unable to successfully rear a cuckoo because they have an inaccessible nest or an unsuitable diet or that have never been recorded to be parasitized (Brooker and Brooker, 1989b). Most of the experiments were performed in Campbell Park and the Australian National Botanic Gardens, Canberra. Brown songlark experiments were performed on grasslands near Hillston in south-western New South Wales by M.M. Red-capped robin experiments were carried out in Terrick Terrick National Park, northern Victoria, by D.K.D.

Model eggs

We presented hosts with a model or real egg that matched their own eggs in size but which differed in color. Following the procedure of Brooker and Brooker (1989a), we selected bright blue ("cobalt turquoise [153]" Daler-Rowney acrylic paint) as the color for the test eggs because this is a conspicuous color that is unlike the egg color of any of the hosts used in this experiment. Model eggs were made of Alumilite Super Plastic cast in silicone molds. We used host eggs that had failed to hatch to make the silicone molds for the models, so that they matched host egg size.

We considered the possibility that the small bill size of small host species may constrain their ability to grasp and reject hard plastic eggs, so we also tested five small Australian species (superb fairy-wrens, yellow-rumped thornbills, buff-rumped thornbills, brown thornbills, red-browed firetails) with real eggs that provided the option of puncture removal (Rohwer and Spaw, 1988). Real eggs were collected from any deserted clutches or from captive zebra finch *Taeniopygia guttata* clutches and painted with the same blue paint (see Langmore et al., 2003). The eggs used in the experiments had all been laid during the previous 9 days.

Artificial parasitism experiment

We followed the general procedure of Moksnes et al. (1991). A single model egg was added to the clutch during egg laying or incubation. No host eggs were removed as egg removal has not been found to influence the probability of model egg rejection in similar experiments (Brooker and Brooker, 1989a; Davies and Brooke, 1988; Moksnes and Røskaft, 1989; Sealy, 1992). The model egg was left in the nest for five full days and removed on the sixth day if it had not been ejected. Nests that were depredated before the full 5 days had elapsed were excluded. The outcome of the trial was scored as (1) acceptance, if the clutch, including the experimental egg, was warm and/or the host was incubating or (2) rejection, which involved two types of behavior: desertion, if the eggs were cold; or ejection, if the bird had either ejected or damaged the experimental egg or some of its own eggs. Only those species for whom at least five trials were successfully completed were included in the data set.

European data

Data were combined from two published studies on responses to nonmimetic eggs in European passerines (Davies and Brooke, 1989a; Moksnes et al., 1991). Where both studies had tested the same species, an overall rejection rate for that species was calculated from the totaled results of the two studies. The European cuckoo has several races or "gentes," each of which lays an egg of a different color or pattern to match its most common host or hosts. For their nonmimetic trials, both studies used model eggs painted to resemble a European cuckoo egg of a different gens from that which would normally parasitize the host in question.

Variables that potentially explained rates of egg rejection

We analyzed the frequency of nonmimetic egg rejection in relation to the life-history parameters proposed by Brooker and Brooker (1996) to be important in influencing the degree of coevolution between cuckoos and hosts: clutch size, duration of the breeding season (the period in which eggs were laid), and cuckoo/host mass ratio. Where a range of values was given for clutch size, we used the midpoint of the range. We did not include the factor "mobility" (migrant versus resident) because the main effect of migration in this context is to reduce the duration of the breeding season, and

Table 1

Host and nonhost species tested with nonmimetic model eggs, showing for each species the number of trials completed, the model egg-rejection rate and the life-history variables used in the analysis (see text for details)

Common name	Scientific name	Number of nests tested	Percentage rejected	Clutch size	Nest type	Host status	Breeding duration (months)	Log light in nest (lux)	Cuckoo/ host weight	Continent
Silvereye	*Zosterops lateralis*	10	70	3	Open	Rare	3	3.85	2.06	Australia
Sedge warbler	*Acrocephalus schoenobaenus*	5	20	4.98	Open	Common	2	1.61	10.0	Europe
Reed warbler	*Acrocephalus scirpaceus*	55	61.82	3.89	Open	Common	2.5	1.33	9.17	Europe
Willow warbler	*Phylloscopus trochilus*	10	90	6.56	Closed	Rare	2.0	1.47	12.94	Europe
Brown songlark	*Cinclorhamphus cruralis*	13	15.38	3.5	Open	Nonhost	3	—	2.96	Australia
Blackcap	*Sylvia atricapilla*	13	76.92	4.65	Open	Rare	2.0	0.83	6.1	Europe
Swallow	*Hirundo rustica*	10	0	4.4	Closed	Nonhost	3.0	−0.05	5.79	Europe
Great tit	*Parus major*	29	6.9	9.9	Closed	Nonhost	1.5	−0.29	6.11	Europe
Blue tit	*Parus caeruleus*	24	0	11.5	Closed	Nonhost	1.5	−0.52	10.0	Europe
Reed bunting	*Emberiza schoeniclus*	20	95	4.4	Open	Rare	2.5	1.53	5.79	Europe
Chaffinch	*Fringilla coelebs*	31	64.52	4.3	Open	Rare	2.0	1.67	4.5	Europe
Bullfinch	*Pyrrhula pyrrhula*	8	0	4.8	Open	Nonhost	3.5	2.15	4.4	Europe
Linnet	*Carduelis cannabina*	14	0	4.8	Open	Nonhost	3.5	1.46	5.79	Europe
Greenfinch	*Carduelis chloris*	29	24.14	4.83	Open	Nonhost	3.5	1.49	4.07	Europe
Pied wagtail	*Motacilla alba*	38	71.05	5.1	Closed	Common	2.5	0.01	5.5	Europe
Meadow pipit	*Anthus pratensis*	82	36.59	5.42	Open	Common	2.5	1.52	6.11	Europe
House sparrow	*Passer domesticus*	5	0	4	Closed	Nonhost	5.0	0.30	4.07	Europe
Dunnock	*Prunella modularis*	32	3.13	5.1	Open	Common	3.5	1.14	5.5	Europe
Red-browed firetail	*Aegintha temporalis*	18	0	5	Closed	Nonhost	7	2.76	2.3	Australia
Double-barred finch	*Poephila bichenovii*	5	0	4.5	Closed	Nonhost	6	—	2.3	Australia
Wren	*Troglodytes troglodytes*	5	0	5.7	Closed	Common	2.5	−1	12.2	Europe
Starling	*Sturnus vulgaris*	21	23.81	4.75	Closed	Nonhost	2.0	0.53	1.38	Europe
Pied flycatcher	*Ficedula hypoleuca*	23	0	7.45	Closed	Nonhost	1.5	−0.31	9.17	Europe
Robin	*Erithacus rubecula*	25	20	5	—	Common	2.5	0.85	6.88	Europe
Song thrush	*Turdus philemos*	51	62.75	4.7	Open	Rare	4	1.29	1.57	Europe
Blackbird	*Turdus merula*	36	63.89	3.87	Open	Rare	4	1.51	1.1	Europe
Yellow robin	*Eopsaltria australis*	5	60	2.5	Open	Rare	5	3.66	1.21	Australia
Red-capped robin	*Petroica goodenovii*	6	0	3	Open	Common	5	4.41	2.56	Australia
Grey fantail	*Rhipidura fuligonosa*	8	100	3	Open	Common	5	3.9	4.5	Australia
Willie wagtail	*Rhipidura leucophrys*	6	100	2.5	Open	Common	4	4.55	4.16	Australia
Rufous whistler	*Pachycephala rufiventris*	6	100	3	Open	Common	4	4.08	3.46	Australia
Superb fairy-wren	*Malurus cyaneus*	47	10.64	4	Closed	Common	6	2.99	2.3	Australia
Western warbler	*Gerygone fusca*	8	25	2.5	Closed	Rare	2	2.38	3.9	Australia
White-throated warbler	*Gerygone olivacea*	6	0	2.5	Closed	Rare	3	2.62	2.41	Australia
Yellow-rumped thornbill	*Acanthiza chrysorrhoa*	10	10	3.5	Closed	Common	5	1.67	2.3	Australia
Buff-rumped thornbill	*Acanthiza reguloides*	10	0	4	Closed	Common	5	2.57	2.92	Australia
Brown thornbill	*Acanthiza pusilla*	8	12.5	3	Closed	Common	4	2.44	5.75	Australia
New Holland honeyeater	*Phylidonyris novaehollandiae*	6	0	2.5	Open	Rare	2.5	—	4.62	Australia
Red wattlebird	*Anthochaera carunculata*	7	42.9	2.5	Open	Common	5	4.06	0.83	Australia
Eastern spinebill	*Acanthorhynchus tenuirostris*	6	33.33	2.5	Open	Common	4	4.06	8.3	Australia
Swift	*Apus apus*	4	0	2.4	Closed	Nonhost	1	−1.0	2.62	Europe

we considered this to be covered by the variable "breeding season duration." We also included the factor host status, with species classified as common hosts (species classified as "biological hosts" in Brooker and Brooker 1989b), rare hosts (species suitable as hosts and with occasional records of parasitism), or nonhosts (species unsuitable as hosts or with no records of parasitism) from Brooker and Brooker (1989b). The same classifications were obtained for the European species from Davies and Brooke (1989a) and Moksnes et al. (1991). Previous work had shown that dome-nesting superb fairy-wrens could detect an egg that was too large but not an egg of the wrong color, suggesting that tactile cues, but not visual cues, are used for egg recognition in dark nest interiors (Langmore et al., 2003). We therefore considered the influence of visibility in the nest on the likelihood of egg rejection. We quantified visibility for as many species as possible by measuring light availability (lux) inside the nest with a Kyoritsu illuminometer 5200 (Australia) and a photographic light meter (U.K.: see Kilner and Davies, 1998 for details). Light environments in Australia are generally far brighter than those in Northern Europe, so it is possible that a domed Australian nest is better illuminated than a cup nest in Northern Europe. To see whether nest type per se also influenced egg-rejection behavior, we classified each species as an "open nester" or a "closed nester," using criteria specified in Kilner (1999). Closed nests included dome-shaped nests and cavity nests.

Clutch sizes for Australian species were taken from Slater et al. (1986). Breeding dates for Canberra species were obtained from Frith and Watts (1984), Taylor (1992), and from our own data in Campbell Park. Average breeding dates for brown songlarks were provided by M.M. and for

Table 2

Species level analysis of the influence of life-history variables on egg-rejection behavior using a general linear model

	df	*F*	*p*	Marginal *F* value
(A) Term in model[a]				
Intercept	1	4.201	.048	
Host status	2	10.607	.000	
Log light	1	12.625	.001	
Cuckoo mass	1	16.736	.000	
Error	33			
Total	38			
(B) Term not included in minimal model[b]				
Duration of breeding season				0.105
Clutch size				0.054
Cuckoo/host mass				0.000
Host mass				0.142
Nest type				0.636

[a] The minimal model is shown.

[b] The terms that were not included in the minimal model, in the sequence in which they were deleted from the model, and their marginal *F* values.

red-capped robins by Dowling (2003). Some Australian hosts are parasitized by more than one species of cuckoo. In these cases we calculated the relative body weight of cuckoo to host for the cuckoo species with the highest number of records of parasitism in Brooker MG and Brooker LC (1989b). For nonhost species we assigned the body weight of the cuckoo that parasitizes similar-sized species; for brown songlarks we assigned pallid cuckoos *Cuculus pallidus*, which parasitize similar-sized, cup-nesting hosts; for Australian finches we assigned shining bronze-cuckoos *Chalcites lucidus*, which parasitize similar-sized, dome-nesting hosts; and for the European non-hosts we considered the European cuckoo *C. canorus* as the only possible parasite. Body weights were obtained from Brooker and Brooker (1989b). Clutch sizes, breeding dates, and body weights for European hosts were taken from Cramp (1985–1992) and Cramp and Perrins (1993–1994), and we used the weight of the European cuckoo given in Davies (2000).

Comparative analysis

We used a general linear model to attempt to explain variation in model egg-rejection rates at the species level. Initially, we included the covariates clutch size, breeding season duration, cuckoo mass, host mass, cuckoo/host mass, log light availability in the nest, and the factors nest type (open or closed) and host status (common host, rare host, or nonhost). We sequentially deleted the least significant term in the model until we were left with only significant terms (the minimal model) at a 0.05 probability criterion.

We repeated the analysis using the independent contrasts method to control for common phylogenetic descent (Felsenstein, 1985) using the comparative analysis by independent contrasts (CAIC) software program (Purvis and Rambaut, 1994). The program calculates contrasts (the direction and magnitude of change) in traits at evolutionarily independent nodes in the phylogeny. Branch lengths were set as equal, which makes all comparisons equally influential. The molecular phylogeny of Sibley and Ahlquist (1990) was used for the analysis (rather than a phylogeny based on morphology or behavior) because it is independent of the traits being investigated. We performed a multivariate analysis, including all the terms we had used in the species-level analysis except nest type (the program will only allow inclusion of one dichotomous variable), and calculated contrasts by overriding the BRUNCH algorithm and by using CRUNCH. A minimal model was achieved by sequentially deleting the least significant term in the model.

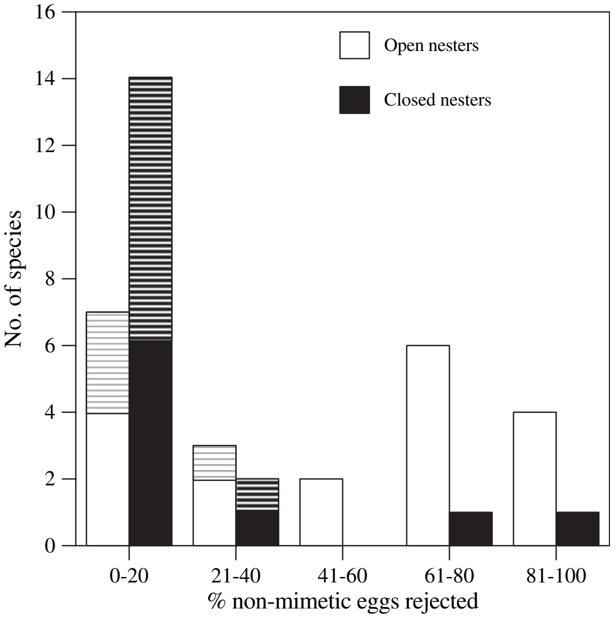

Figure 1
Percentage of model eggs rejected for open-nesting species (white bars) and closed-nesting species (black bars). Striped sections of bars indicate nonhost species.

RESULTS

Rejection of nonmimetic eggs by Australian hosts ranged from 0% to 100% (Table 1). Like Brooker and Brooker (1989a), we found high rates of acceptance of nonmimetic eggs in thornbills and fairy-wrens. However, we found that other Australian species (e.g., grey fantails and willie wagtails) ejected all nonmimetic eggs. The high acceptance rates of thornbills and fairy-wrens were not caused by an inability to reject the model egg due to their small bill size because rejection rates were not significantly higher when they were given the option of puncture ejection of real, painted eggs (buff-rumped thornbills, 0/2 models and 0/8 real eggs rejected; yellow-rumped thornbills, 1/3 model and 1/7 real eggs rejected; brown thornbills, 1/4 model and 0/4 real eggs rejected; red-browed firetails, 0/12 model and 0/6 real eggs rejected; superb fairy-wrens, 3/22 model and 3/16 real eggs rejected, Fisher's Exact test, all $p > .65$).

Analysis of species data

Only three independent variables were retained in the minimal model: host status, light availability, and cuckoo mass (Table 2), and together they explained 54.1% of the variation in egg rejection by hosts. Rejection rates did not differ significantly between common and rare hosts (Fisher's PLSD, NS), but both were greater than rejection rates of nonhosts (Fisher's PLSD, $p < .01$ in both cases). Therefore, common and rare hosts were combined in the subsequent analyses using independent contrasts. Rejection rates were also greater in lighter nests than darker nests (Figure 1) and

Table 3

Univariate analyses of both the species data and the contrast data

Term	Species data		Contrast data	
		P		p
Host status	$F_{2,38} = 8.83$	.001	$t_8 = 4.02$	.004
Log light	$F_{1,37} = 5.98$	.019	$F_{1,32} = 3.20$	.083
Cuckoo mass	$F_{1,40} = 0.556$	.460	$F_{1,35} = 0.20$	.654
Nest type	$F_{1,39} = 10.74$	.002	$T_7 = 1.27$	.246
Clutch size	$F_{1,40} = 1.85$	.182	$F_{1,35} = 1.94$	.173
Breeding season duration	$F_{1,40} = 0.553$	.462	$F_{1,34} = 1.79$	.190
Host mass	$F_{1,40} = 0.973$	.330	$F_{1,35} = 2.46$	.126
Cuckoo/host mass	$F_{1,40} = 0.034$	.855	$F_{1,35} = 0.38$	.543

The significant terms from the minimal model describing the species data are shown in bold.

Table 4

Multivariate analysis of the contrast data, examining the influence of life-history variables on rejection rates

	df	F	p	Marginal F value
(A) Term in model[a]				
Host status	1	13.22	.001	
Error	30			
Total	31			
(B) Term not included in minimal model[b]				
Cuckoo mass				0.027
Clutch size				0.860
Cuckoo/host mass				2.144
Duration of breeding season				0.195
Log light				0.928
Host mass				2.983

[a] The minimal model.

[b] Terms that were not included in the minimal model, in the sequence in which they were deleted from the model, and their marginal F values.

in hosts parasitized by larger cuckoos than by hosts parasitized by smaller cuckoos. None of the life-history parameters (clutch size, breeding season duration, cuckoo/host body weight) could explain a significant amount of the variation in model egg-rejection rates. Nor was there a significant interaction between any of the terms in the minimal model.

We also performed univariate analyses to look at the separate relationships between each variable in the multivariate analysis and rates of egg rejection (Table 3). The results differed from those generated by the multivariate analysis in two key respects. First, cuckoo mass alone could not explain a significant amount of variation in host egg rejection: its effect was therefore only apparent in the multivariate analysis because nest light availability and host status were controlled statistically. Second, nest type accounted for host egg-rejection habits, with "open nesters" more likely to reject odd-looking eggs than "closed nesters." The results of the multivariate analysis suggest that this correlation is best explained by differences in light availability between the two nest types rather than by contrasting nest architectures.

Analysis of independent contrasts

The multivariate analysis of independent contrasts showed that host status (host versus nonhost) alone accounted for a significant amount of variation in egg rejection (Table 4). Neither nest light availability nor cuckoo mass was significantly related to rates of egg rejection, even though both variables were retained in the minimal model that explained the species data. Again no life-history parameters were significant in the multivariate analysis.

We also performed univariate analyses of the contrast data (Table 3) for comparison with the equivalent analyses of the species data. Of all the variables in the minimal model describing the species data, only "host status" could significantly account for variation in egg-rejection behavior, although the relationship with nest light availability was marginally nonsignificant. No other variable was correlated significantly with rates of egg rejection.

DISCUSSION

The most significant factor explaining rates of rejection of nonmimetic eggs in the nest was whether or not a species was a cuckoo host. The effect was strong and persisted after controlling for common phylogenetic descent. The result supports the coevolution model of cuckoo-host interactions because it demonstrates that egg-rejection behavior has evolved in response to parasitism by cuckoos. Furthermore, it suggests that parasitism is always sufficiently costly to provoke the evolution of host defenses, given enough evolutionary time. No life-history strategy that we analyzed consistently reduced the cost of parasitism sufficiently to explain patterns of host egg acceptance.

After controlling for common phylogenetic descent, no other variable was significant. However, at the species level, after controlling for the possibility of parasitism, light availability in the nest and nest type were the next best predictors of rejection rates (Figure 1). The effect of nest type disappears after controlling for nest light availability, so illumination within the nest is the key feature that predicts egg rejection. This finding is unsurprising because discrimination between eggs on the basis of color or pattern (the distinguishing characteristics of the model eggs) requires adequate visibility. Moreover, several studies of dome-nesting hosts indicate that in dark nest interiors, hosts are more likely to rely on tactile cues than visual cues to discriminate parasitic eggs (Langmore et al., 2003; Marchetti, 2000; Mason and Rothstein, 1986). In a previous study, four Australian and New Zealand hosts accepted model eggs, and this result was attributed to the common life-history variables of the hosts (Brooker and Brooker, 1996). However, all these hosts build dome-shaped nests and our analysis suggests that the dark nest interior is a more likely explanation for the high acceptance rates of these hosts.

The significant effect of light availability on the likelihood of egg rejection at the species level indicates that the rate of egg rejection may be constrained by its cost. Poor visibility in the nest may limit host ability to recognize foreign eggs amongst their clutch, increasing the risk of recognition errors and thereby resulting in an evolutionary equilibrium favoring cuckoo egg acceptance at low rates of parasitism.

A third variable, cuckoo mass, also predicted the incidence of egg rejection at the species level, but only after taking into account host status and nest light availability. This result is not easy to explain. At first sight, it appears to support the life-history hypothesis, which predicts that a larger parasite will increase the costs of parasitism and so provoke the evolution of host defenses against parasitism (Brooker and Brooker 1996). However, presumably greater costs are borne by hosts that are relatively small in relation to the cuckoo, yet we could detect no relationship between cuckoo/host mass and the incidence of model egg rejection. Furthermore, the effect of cuckoo mass disappeared after controlling for common phylogenetic descent. Perhaps the correlation with cuckoo mass is simply an artifact of a correlation with a third, unknown geographical variable because hosts in Europe are exploited by a cuckoo species that is larger than those that victimize most Australian host species. The significant effect of cuckoo mass and not of cuckoo/host mass may also be explained by nest type because all but one of the cup-nesting hosts are parasitized by large cuckoos.

Our analysis at the species level explained 54.1% of the variation in host egg-rejection rates. The remaining 45.9% of variation might be accounted for by factors we could not quantify, such as variation in the parasitism rates experienced by the host populations used in the experiments, the duration of host-parasite coevolution, or the breeding experience of the individuals used in the experiments (because egg recognition appears to be learned in the first breeding attempt, Lotem et al., 1992, 1995). Further, some hosts may use defenses other than egg rejection against brood parasites, including nest defense (Soler et al., 1999) or rejection of cuckoo chicks rather than cuckoo eggs (Langmore et al., 2003). Life-history variables may be better able to explain variation among hosts in these defenses than in their ability to reject odd-looking eggs.

In summary, by collecting new data on egg-rejection rates from Australian hosts, we were able to test the role of life-history variables in explaining variation in egg-rejection rates between species more comprehensively than was possible in previous analyses. Like Soler's (1999) analysis of rejection rates in the hosts of the European cuckoo, we found little support for the life-history hypothesis for egg rejection. Our results suggest that parasitism is always sufficiently costly to select for host defenses, and no life-history strategy can fully offset those costs. We suggest that variation in egg-rejection rates between species is better explained by the recognition costs associated with egg rejection. Hosts with dark nests are unable to see the cuckoo egg clearly in their nest and accept foreign eggs to avoid mistakenly rejecting their own. Although our study suggests that life-history variables are not the primary explanation for variation in rejection rate, it is still possible that differences in life history between species may contribute to differences in the equilibrium point at which egg rejection evolves. Thus, a life-history strategy that makes parasitism less costly may increase the probability that the cost of recognition errors will offset the potential benefits of rejection.

N.E.L. was supported by an Australian Research Council Postdoctoral Fellowship and an Australian Academy of Science J.G. Russell Award. R.M.K. was supported by a Royal Society Dorothy Hodgkin Research Fellowship and a Royal Society University Research Fellowship. N.B.D. and S.H.B. were supported by a Natural Environment Research Council research grant. Many thanks to M. Hauber and A Lotem for helpful comments on the manuscript.

REFERENCES

Blackburn TM, Gaston KJ, 1998. Some methodological issues in macroecology. Am Nat 151:68–83.

Brooke M de L, Davies NB, 1988. Egg mimicry by cuckoos *Cuculus canorus* in relation to discrimination by hosts. Nature 335:630–632.

Brooker MG, Brooker LC, 1989a. The comparative breeding behaviour of two sympatric cuckoos, Horsfield's Bronze-Cuckoo *Chrysococcyx basalis* and the Shining Bronze-Cuckoo *C. lucidus*, in western Australia: a new model for the evolution of egg morphology and host specificity in avian brood parasites. Ibis 131:528–547.

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

Brooker MG, Brooker LC, 1996. Acceptance by the Splendid Fairy-Wren of parasitism by Horsfield's Bronze-cuckoo: further evidence for evolutionary equilibrium in brood parasitism. Behav Ecol 7: 395–407.

Chance EP, 1940. The truth about the cuckoo. London: Country Life.

Cramp S, 1985–1992. The birds of the Western Palearctic, vols. 5–7. Oxford: Oxford University Press.

Cramp S, Perrins CM, 1993–1994. The birds of the Western Palearctic, vols. 8–9. Oxford: Oxford University Press.

Davies NB, 2000. Cuckoos, cowbirds and other cheats. London: T & AD Poyser.

Davies NB, Brooke M de L, 1988. Cuckoos versus reed warblers: adaptations and counteradaptations. Anim Behav 36:262–284.

Davies NB, Brooke M de L, 1989a. An experimental study of co-evolution between the cuckoo, *Cuculus canorus*, and its hosts. I. Host egg discrimination. J Anim Ecol 58:207–224.

Davies NB, Brooke M de L, 1989b. An experimental study of co-evolution between the cuckoo, *Cuculus canorus*, and its hosts. II. Host egg markings, chick discrimination and general discussion. J Anim Ecol 58:225–236.

Davies NB, Brooke M de L, Kacelnik A, 1996. Recognition errors and probability of parasitism determine whether reed warblers should accept or reject mimetic cuckoo eggs. Proc R Soc Lond B 263: 925–931.

Dawkins, R, Krebs JR, 1979. Arms races between and within species. Proc R Soc Lond B 205:489–511.

Dowling DK, 2003. Breeding biology of the red-capped robin. Aust J Zool 51:533–549.

Duckworth JW, 1991. Responses of breeding reed warblers *Acrocephalus scirpaceus* to mounts of sparrowhawks *Accipiter nisus*, cuckoo *Cuculus canorus* and jay *Garrulus glandarius*. Ibis 133:68–74.

Felsenstein J, 1985. Phylogenies and the comparative method. Am Nat 125:1–15.

Frith HJ, Watts BT, 1984. Birds in the Australian high country. Melbourne: Angus & Robertson Publishers.

Higuchi H, 1998. Host use and egg color of Japanese cuckoos. In: Parasitic birds and their hosts (Rothstein SI, Robinson SK, eds). Oxford: Oxford University Press; 80–93.

Hosoi, SA, Rothstein SI, 2000. The enigma of nest desertion: is it really a defense against cowbird parasitism? Anim Behav 59: 823–840.

Kilner RM, 1999. Family conflicts and the evolution of nestling mouth color. Behaviour 136:779–804.

Kilner RM, Davies NB, 1998. Nestling mouth color: ecological correlates of a begging signal. Anim Behav 56:705–712.

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

Lotem A, Nakamura H, 1998. Evolutionary equilibria in avian brood parasitism: an alternative to the 'arms race–evolutionary lag' concept. In: Parasitic birds and their hosts (Rothstein SI, Robinson SK, eds). Oxford: Oxford University Press; 223–235.

Lotem A, Nakamura H, Zahavi A, 1992. Rejection of cuckoo eggs in relation to host age: a possible evolutionary equilibrium. Behav Ecol 3:128–132.

Lotem A, Nakamura H, Zahavi A, 1995. Constraints on egg discrimination and cuckoo-host co-evolution. Anim Behav 49: 1185–1209.

Marchetti K, 2000. Egg rejection in a passerine bird: size does matter. Anim Behav 59:877–883.

Mason P, Rothstein SI, 1986. Coevolution and avian brood parasitism: cowbird eggs show evolutionary response to host discrimination. Evolution 40:1207–1214.

Moksnes A, Røskaft E, 1989. Adaptations of meadow pipits to parasitism by the common cuckoo. Behav Ecol Sociobiol 24:25–30.

Moksnes A, Røskaft E, Braa AT, Korsnes L, Lampe H, Pedersen HC, 1991. Behavioural responses of potential hosts towards artificial cuckoo eggs and dummies. Behaviour 116:64–89.

Price T, 1997. Correlated evolution and independent contrasts. Philos Trans R Soc Lond B 352:519–529.

Purvis A, Rambaut A, 1994. Comparative analysis by independent contrasts (CAIC), version 2. Oxford: Oxford University.

Rohwer S, Spaw CD, 1988. Evolutionary lag versus bill-size constraints: a comparative study of the acceptance of cowbird eggs by old hosts. Evol Ecol 2:27–36.

Rothstein SI, 1990. A model system for coevolution: avian brood parasitism. Annu Rev Ecol Syst 21:481–508.

Rothstein SI, Robinson SK, 1998. Parasitic birds and their hosts: studies in coevolution. Oxford: Oxford University Press.

Schluter D, 2000. The ecology of adaptive radiations. Oxford Series in Ecology and Evolution. Oxford: Oxford University Press.

Sealy SG, 1992. Removal of yellow warbler eggs in association with cowbird parasitism. Condor 94:40–54.

Sibley CG, Ahlquist JE, 1990. Phylogeny and classification of birds. Yale: Yale University Press.

Slater P, Slater P, Slater R, 1986. The slater field guide to Australian birds. Willoughby: Weldon Publishing.

Soler JJ, 1999. Do life-history variables of European cuckoo hosts explain their egg-rejection behavior? Behav Ecol 10:1–6.

Soler JJ, Soler M, Perez-Contreras T, Aragon S, Møller AP, 1999. Antagonistic antiparasite defenses: nest defense and egg rejection in the magpie host of the great spotted cuckoo. Behav Ecol 10: 707–713.

Takasu F, Kawasaki K, Nakamura H, Cohen JE, Shigesada N, 1993. Modeling the population dynamics of a cuckoo-host association and the evolution of host defences. Am Nat 142:819–839.

Taylor M, 1992. Birds of the Australian capital territory, an Atlas. Canberra: Canberra Ornithologists Group & National Capital Planning Authority.