REJECTION BEHAVIOR BY COMMON CUCKOO HOSTS TOWARDS ARTIFICIAL BROOD PARASITE EGGS

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ABSTRACT.—We studied the rejection behavior shown by different Norwegian cuckoo hosts towards artificial Common Cuckoo (*Cuculus canorus*) eggs. The hosts with the largest bills were grasp ejectors, those with medium-sized bills were mostly puncture ejectors, while those with the smallest bills generally deserted their nests when parasitized experimentally with an artificial egg. There were a few exceptions to this general rule. Because the Common Cuckoo and Brown-headed Cowbird (*Molothrus ater*) lay eggs that are similar in shape, volume, and eggshell thickness, and they parasitize nests of similarly sized host species, we support the puncture resistance hypothesis proposed to explain the adaptive value (or evolution) of strength in cowbird eggs. The primary assumption and prediction of this hypothesis are that some hosts have bills too small to grasp parasitic eggs and therefore must puncture-eject them, and that smaller hosts do not adopt ejection behavior because of the heavy cost involved in puncture-ejecting the thick-shelled parasitic egg. We compared our results with those for North American Brown-headed Cowbird hosts and we found a significantly higher proportion of rejecters among Common Cuckoo hosts with grasp indices (i.e. bill length × bill breadth) of <200 mm^2. Cuckoo hosts ejected parasitic eggs rather than accept them as cowbird hosts did. Among the Common Cuckoo hosts, the cost of accepting a parasitic egg probably always exceeds that of rejection because cuckoo nestlings typically eject all host eggs or nestlings shortly after they hatch. *Received 25 February 1990, accepted 23 October 1990.*

THE EGGS of many brood parasites have thicker shells than the eggs of other bird species of similar size (Lack 1968, Spaw and Rohwer 1987). Several hypotheses have been developed to explain this phenomenon, the most recent being that of Spaw and Rohwer (1987). Spaw and Rohwer (1987) and Rohwer and Spaw (1988) argued that the thick eggshell of the parasitic American cowbird (*Molothrus*) species has evolved so as to resist puncture ejection by small host species. They tested an assumption of this hypothesis by measuring the length and the width of the bill (the product of these two measurements they termed the "grasp index") of Brown-headed Cowbird (*M. ater*) hosts which had been classified as acceptors or rejecters. They concluded that some small-sized hosts are more or less forced to be acceptors because of heavy cost involved in getting rid of the thick-shelled Brown-headed Cowbird egg. This hypothesis has received support from Picman (1989) and Rohwer et al. (1989).

Rothstein (1975, 1976, 1977) showed that, although many parasitized species accepted (or did not remove) introduced nonmimetic artificial eggs of Brown-headed Cowbirds, some species ejected them. He observed and inferred that these potential hosts ejected eggs from their nests either by grasping the eggs or by puncturing the eggs before removal. Rohwer and Spaw (1988) used this distinction in ejection type when they considered the possibility of physical constraints to ejection for those species parasitized by Brown-headed Cowbirds. They compared the characteristic type of ejection (grasp or puncture) or lack of ejection response (acceptance) with the bill size for each of 40 parasitized passerine species. They suggest that small bill size constrains some species from grasping the cowbird eggs for ejections, and that the strength of the cowbird eggs limits successful puncture ejections for most of these species. Rohwer and Spaw (1988) propose that the costs associated with these constraints have selected for acceptance. It is not clear from their indirect test which acceptor species are capable of successfully puncturing cowbird eggs for ejections (and would do so, given sufficient selective pressure) and which acceptor species cannot puncture the cowbird egg because the eggshell is too strong.

So far only one host species of the North American Brown-headed Cowbird, the Northern Oriole (*Icterus galbula*), has been shown to be a true puncture ejector (Rothstein 1977). To test whether Northern Orioles experience any

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cost in puncture-ejecting the thick-shelled Brown-headed Cowbird egg, Rohwer et al. (1989) added Brown-headed Cowbird and control eggs into oriole nests, and found that the host species occasionally damaged some of its own eggs in the process of ejecting the cowbird egg.

The Common Cuckoo (*Cuculus canorus*) is the most abundant brood parasite in Europe, and eggs from this species have been reported from nests of >100 different host species, but cuckoo chicks have not been observed in nests of all these potential hosts (Baker 1942, Lack 1968, Wyllie 1981). Unlike the Brown-headed Cowbird, the Common Cuckoo is regarded as a host specialist, laying eggs that normally mimic those of the hosts. Because successful parasitism by the cuckoo reduces the host's breeding success dramatically, natural selection will be expected to favor host defense mechanisms that reduce the probability of being parasitized (Davies and Brooke 1989, Moksnes et al. 1991).

Davies and Brooke (1989) and Moksnes et al. (1991) have shown that many species parasitized by the Common Cuckoo discriminate and reject nonmimetic artificial cuckoo eggs experimentally introduced into their nests. Furthermore, cuckoo hosts with shorter bills were more likely to reject by desertion, while species with longer bills ejected cuckoo eggs (Davies and Brooke 1989).

We parasitized experimentally 19 Common Cuckoo hosts with artificial cuckoo eggs and 3 hosts with artificial or natural conspecific eggs. We recorded the rejection behavior of the hosts. From the results of these experiments, we evaluated, with comparative analysis, possible physical constraints in rejection behavior of small bill size. Finally, we compared our results with those reported for cowbird hosts.

If we assume that cuckoo eggs are similar in size, shape, and eggshell thickness (strength) to those of cowbirds, and that the most commonly parasitized species are small passerines, it is reasonable to expect that potential cuckoo hosts experience similar constraints in ejection behavior. However, unlike cowbird hosts, which may successfully raise some of their own offspring along with the cowbird nestling (e.g. Mayfield 1961, Rothstein 1975, Clark and Robertson 1981), there is little reproductive success to a host that accepts a cuckoo egg because cuckoo nestlings normally eject all host eggs or nestlings shortly after they hatch. Costs of acceptance should therefore strongly select for an ejection response in those species capable of ejecting cuckoo eggs (Davies and Brooke 1989). One prediction for Common Cuckoo hosts is that large-billed hosts, which can grasp the parasitic egg and eject it, would be expected to do so; intermediate-billed hosts, which cannot grasp the parasitic egg, should puncture-eject; and hosts with the smallest bills, which cannot eject the parasitic egg, will desert the nest. The threshold for initiating ejection behavior should be lower for cuckoo hosts than for cowbird hosts.

MATERIAL AND METHODS

The fieldwork of this study was carried out in both mountain and lowland areas in Central Norway (Moksnes and Røskaft 1987, 1988, 1989; Moksnes et al. 1991).

We introduced artificial cuckoo eggs into the nests of 19 species. The eggs were made of araldite (a hard plastic) to which a small amount of fiberglass powder as well as ground color, matching that of normal cuckoo eggs, had been added. The eggs were cast in lead molds lined with a layer of silicone rubber. A mixture of glycerol and albumen was injected into the eggs. Afterwards they were painted to resemble cuckoo eggs. They were of the same size and weight as natural Common Cuckoo eggs (for a more detailed description, see Moksnes and Røskaft 1988, 1989). The plastic eggs were, however, more resistant to destruction than natural ones; very few of the host species were able to puncture these artificial eggs. The species were parasitized with eggs painted to resemble different host species, and could therefore be mimetic or nonmimetic compared with those of the host eggs. We report only those cases where rejection occurred.

We carried out the experiments during the egg-laying and incubation periods in 1986–1990. During the egg-laying period the eggs were exchanged after the host had laid its fourth egg. Because of difficulties in locating nests during the laying period, some of the artificial parasitism experiments had to be made during the incubation period also (see Moksnes and Røskaft [1989] and Moksnes et al. [1991] for the distribution of these experiments according to the laying and incubation periods of the hosts). There was no difference in the rejection behavior according to stage in the incubation period, but some species tended to accept at a higher rate during the last days before hatching (Moksnes et al. 1991; but see also Davies and Brooke 1989). When nests were first visited, we recorded the number of host eggs. The eggs were floated (Hays and Lecroy 1971) to determine if they were freshly laid or had been incubated. By floating the eggs or by examining the embryos, we were able to estimate the laying dates for each of the nests in our sample.

Rejection behavior towards artificial and conspecific eggs.—We removed one of the host eggs and added either one mimetic or one nonmimetic plastic Common Cuckoo egg. In the Brambling (*Fringilla montifringilla*) and the Common Chaffinch (*F. coelebs*), we performed additional experiments with plastic eggs similar to conspecific eggs in size and color patterns. Each nest was then visited every second day for at least 6 days after the artificial egg was introduced. If no rejection behavior was observed by the sixth day, the parasitic egg was considered accepted (Moksnes et al. 1991).

Because the plastic eggs were difficult for the host to puncture-eject, we observed only three different patterns of rejection behavior: (1) The artificial egg was removed from the nest, and all the host's eggs remained unharmed. Such behavior was defined as *selective ejection.* (2) The artificial egg was either removed from the nest or left in the nest. In both cases however, one, several, or all of the host's eggs were destroyed or removed. In the majority of such cases, the artificial egg was left in the nest. Such rejection behavior was defined as *unselective ejection,* irrespective of whether or not the host subsequently deserted its nest. (3) The nest was abandoned, but the nest contents were left unharmed. Such rejection behavior was defined as *desertion.*

Rothstein (1975) found that rejection or acceptance behavior by Brown-headed Cowbird hosts was normally an all-or-none response. However, in some Common Cuckoo hosts, this pattern is not so clear (Davies and Brooke 1989, Moksnes et al. 1991). We classified a species as an acceptor when a nonmimetic artificial cuckoo egg was accepted in >50% of the experiments (Moksnes et al. 1991). Furthermore, classification as a selective/unselective ejector, or deserter, depended on how the majority (see Table 1) of the rejecting individuals behaved, regardless of whether the species as a whole was an acceptor or not.

For three species—the Brambling, the Common Chaffinch, and the Common Reed-Bunting (*Emberiza schoeniclus*)—some further experiments were carried out using natural conspecific eggs. The same definitions in rejection behavior were used as for artificial eggs.

Bill size and egg morphology.—We measured the females of the host species (taken from museum collections) by Rohwer and Spaw's (1988) method, to record their grasp-index values. Tomial length was determined from the commissural point at the corner of the mouth, diagonally to the tip of the upper mandible (to ±0.1 mm). Bill breadth was the distance between the commissural points (to ±0.1 mm, Rohwer and Spaw 1988). Grasp index is the tomial length multiplied by the commissural breadth. Except for two species, five females of each species were measured.

We measured egg length and breadth on 424 Common Cuckoo eggs in the collections of different Scandinavian museums. Egg volume was estimated by the formula (Hoyt 1979), $V = 0.51 \cdot \text{length} \cdot \text{breadth}^2 \cdot 1{,}000^{-1}$. In addition egg shape was estimated according to the formula, egg shape = length/breadth (Picman 1989).

Eggshell thickness was measured to the closest 0.001 mm with a Model 35 Federal Bench Comparator thickness gauge (see Spaw and Rohwer 1987, for a closer description of this method).

RESULTS

Egg rejection.—We tested the rejection behavior of 19 species toward the artificial Common Cuckoo egg. Of these, 6 species were selective ejectors, 7 were unselective ejectors, and 6 were deserters (Table 1).

Bramblings ($n = 20$), chaffinches ($n = 13$), and reed-buntings ($n = 3$) were also tested with conspecific eggs of normal size and eggshell thickness. All 36 were rejected, 23 by selective ejections. After ejection, in one nest of each species one of the host's eggs was missing along with the parasitic egg. In another Brambling nest, one of the host's own eggs was missing. These four rejections were classified as unselective ejections. The remaining nests were deserted.

The Brambling and the Common Chaffinch were also tested with artificial plastic eggs that mimicked conspecific eggs. In the Brambling, rejections occurred in 7 of 10 experiments. In the Common Chaffinch, 8 of 11 experiments produced rejection, all by unselective ejection.

Egg morphology.—Brown-headed Cowbird and Common Cuckoo eggs are similar in many respects. The eggshell thickness of Common Cuckoo eggs is 0.108 mm (SD = 0.005, $n = 10$) or slightly thinner than that of the Brown-headed Cowbird (0.110 mm, Spaw and Rohwer 1987; 0.125 mm, Picman 1989). The eggshells of both the cuckoo and the cowbird are thicker than comparable species (cf. Spaw and Rohwer 1987). On average, cuckoo egg volume (3.078 cm^3; SD = 0.467, $n = 424$) is a little larger than that of the Brown-headed Cowbird (2.838 cm^3; Picman 1989). The general shape of the Common Cuckoo and Brown-headed Cowbird egg is similar, although the cuckoo egg is slightly longer (Common Cuckoo: 1.337 ± 0.072 cm, $n = 424$; Brown-headed Cowbird: 1.306 cm, Bent 1958; 1.296 cm, Picman 1989).

Grasp index.—The smallest grasp ejector (the Cedar Waxwing, *Bombycilla cedrorum*) among the North American Brown-headed Cowbird hosts

TABLE 1. Rejection behavior of different host species towards artificial Common Cuckoo eggs. Abbreviations: n = number of rejections observed, S = selective ejection, U = unselective ejection, D = desertion, RS = reaction status of the species, % A = percentage of acceptance of nonmimetic cuckoo eggs as reported by Moksnes et al. (1991), A = acceptor, R = rejecter (for terms see Material and Methods).

Species	n	S	U	D	RS (% A)
Selective ejectors					
Fieldfare (*Turdus pilaris*)	3	2	—	1	A (91)
Song Thrush (*T. philomelos*)	8	7	—	1	R (20)
Blackbird (*T. merula*)	2	2	—	—	R (0)
Redwing (*T. iliacus*)	25	22	—	3	A (65)
Spotted Flycatcher (*Muscicapa striata*)[1]	6	4	1	1	R (56)
Bluethroat (*Luscinia svecica*)	14	14	—	—	R (47)
Unselective ejectors					
Garden Warbler (*Sylvia borin*)	3	—	3	—	R (33)
Blackcap (*S. atricapilla*)	15	—	11	4	R (23)
Icterine Warbler (*Hippolais icterina*)	5	1	2	2	R (33)
Common Chaffinch (*Fringilla coelebs*)	24	2	15	7	R (31)
Brambling (*F. montifringilla*)	40	4	28	8	R (10)
Yellowhammer (*Emberiza citrinella*)	8	1	4	3	R (0)
Common Reed-Bunting (*E. schoeniclus*)	21	1	16	4	R (9)
Deserters					
Meadow Pipit (*Anthus pratensis*)	20	—	1	19	A (92)
Yellow Wagtail (*Motacilla flava*)	4	—	1	3	R (20)
White Wagtail (*M. alba*)	3	—	—	3	R (0)
European Greenfinch (*Carduelis chloris*)	7	—	2	5	A (59)
Willow Warbler (*Phylloscopus trochilus*)	20	—	1	19	R (10)
Chiff Chaff (*P. collybita*)	6	—	1	5	R (0)
Uncertain status					
Dunnock (*Prunella modularis*)[2]	0	—	—	—	A (100)
Lapland Longspur (*Calcarius lapponicus*)	0	—	—	—	A (100)

[1] The Spotted Flycatcher is regarded as a rejecter species because Davies and Brooke (1989) reported 90% rejection in this species.

[2] The Dunnock has an uncertain-rejecter status in our sample, but Davies and Brooke (1989) reported two cases of desertion in the species.

has a grasp index ca. 230 mm^2 (Rohwer and Spaw 1988). All four species in our sample with a grasp index of >230 mm^2 were selective ejectors (Table 2). The Bluethroat (*Luscinia svecica*; index = 131.1 mm^2) and the Spotted Flycatcher (*Muscicapa striata*; index = 179.3 mm^2) were selective ejectors. These grasp-index values are far below those of the North American grasp ejectors. The grasp-index value for the Bluethroat is also lower than for some of the unselective ejector species we identified.

All 7 unselective ejectors (Table 1) had grasp indices between 78.8 and 147.9 mm^2 (Table 2). These values are lower than those of the North American puncture-ejector species (Northern Oriole, 176.0 mm^2; Rohwer and Spaw 1988).

The 5 species with the largest grasp indices selectively ejected the artificial Common Cuckoo egg, while the two smallest-billed species in the sample were both deserters (Tables 1, 2). When ranked according to their grasp index and rejection status, the correlation between the largest-billed species and selective ejectors was statistically significant (Mann Whitney U-test; $U = 74$, $n = 6, 13$, $P < 0.001$; Tables 1, 2). Similarly, the finding that the smallest-billed hosts were deserters was almost statistically significant ($U = 61$, $n = 6, 13$, $P < 0.07$). However, when we compared the unselective ejectors with the deserters, we found that the unselective ejectors had grasp indices larger than that of the deserters, but this difference was not statistically significant ($U = 26$, $n = 6, 7$, NS). On the other hand, the findings that the unselective ejectors had grasp indices smaller than that of the selective ejectors was statistically significant ($U = 39$, $n = 6, 7$, $P < 0.01$).

Rejection behavior of cuckoo and cowbird hosts.—We regarded the species—all of which are potential Common Cuckoo hosts (see Moksnes et al. 1991 for definitions of potential hosts)—as small species if grasp indices fell below 200 mm^2. Thirteen were classified as rejecters and only four as acceptors (European Greenfinch,

TABLE 2. Grasp indices and bill-size measurements ($\bar{x}$ ± SD) of different Common Cuckoo hosts. Grasp index is the product of the diagonal length and commisural breadth, n = number of birds measured.

Species	n	Grasp index (mm^2)	Diagonal length (mm)	Commisural breadth (mm)
Selective ejectors				
Fieldfare	5	348.0	25.4 ± 0.7	13.7 ± 0.3
Song Thrush	5	321.3	25.7 ± 0.6	12.5 ± 0.6
Blackbird	5	411.4	29.6 ± 1.3	13.9 ± 0.7
Redwing	5	283.2	24.0 ± 0.6	11.8 ± 0.3
Spotted Flycatcher	5	179.3	18.3 ± 0.9	9.8 ± 0.6
Bluethroat	5	131.1	16.6 ± 0.5	7.9 ± 0.2
Unselective ejectors				
Garden Warbler	5	147.9	15.9 ± 0.4	9.3 ± 0.7
Blackcap	5	135.5	15.4 ± 0.6	8.8 ± 1.1
Icterine Warbler	4	142.7	17.4 ± 0.9	8.2 ± 0.1
Common Chaffinch	5	111.8	13.8 ± 0.5	8.1 ± 0.4
Brambling	5	106.9	13.2 ± 0.5	8.1 ± 0.4
Yellowhammer	5	105.4	12.4 ± 0.4	8.5 ± 0.4
Common Reed-Bunting	5	78.8	10.8 ± 0.3	7.3 ± 0.7
Deserters				
Meadow Pipit	5	118.6	15.4 ± 0.3	7.7 ± 0.3
Yellow Wagtail	5	112.7	16.1 ± 0.6	7.0 ± 0.3
White Wagtail	3	117.9	16.6 ± 0.8	7.1 ± 0.4
European Greenfinch	5	134.4	14.3 ± 0.7	9.4 ± 0.5
Willow Warbler	5	70.9	13.9 ± 0.7	5.1 ± 0.4
Chiff Chaff	5	66.6	12.1 ± 0.5	5.5 ± 0.4
Uncertain status				
Dunnock	5	108.6	15.3 ± 0.4	7.1 ± 0.3
Lapland Longspur	5	88.2	11.6 ± 0.3	7.6 ± 0.2

Carduelis chloris; Meadow Pipit, *Anthus pratensis*; Lapland Longspur, *Calcarius lapponicus*; Dunnock, *Prunella modularis*; Table 1). In Rohwer and Spaw's (1988) sample, 2 of the potential Brown-headed Cowbird hosts with grasp indices of <200 mm^2 were rejecters (i.e. if the Marsh Wren, *Cistothorus palustris*, is also classified as a puncture ejector), and 25 were acceptors. The difference in frequency of rejecters among small-billed European Common Cuckoo hosts (13/17) and North American Brown-headed Cowbird hosts (2/27) is statistically significant (Fisher's exact probabilities test; $P < 0.001$).

DISCUSSION

Rejection behavior.—The use of plastic eggs makes it possible to distinguish between grasp and puncture ejection because the plastic eggs are so resistant to puncture that host's eggs are usually damaged in the process. Rothstein (1975) inferred that most cowbird egg-rejecters used grasp ejection because whole plaster eggs were removed and all host eggs were left intact after ejections. (In Northern Orioles [Rothstein 1977], however, some host's eggs were damaged or removed.) Western Kingbirds (*Tyrannus verticalis*) and American Robins (*Turdus migratorius*) did not damage any of their own eggs when ejecting introduced real Brown-headed Cowbird eggs, whereas Northern Orioles did frequently (Rohwer et al. 1989). In our study, when artificial eggs were rejected from the nest, and all the host's eggs remained unharmed (selective ejection), we interpreted the behavior as grasp ejection, even though there was a possibility that in nature they might have been ejected by puncture ejection. These species may be regarded as grasp ejectors. On the other hand, when attempts to reject artificial eggs resulted in one, several, or all of the host's eggs being destroyed or removed, this destruction was probably the result of repeated attempts to remove the parasitic egg by puncture ejection. This observation is validated by Reed Warblers (*Acrocephalus scirpaceus*) observed pecking on artificial cuckoo eggs (Davies and Brooke 1988). Plausibly, species that unselectively ejected the artificial eggs can be regarded as puncture ejectors. We will use the term grasp or puncture ejectors for those species.

Rejection of conspecific eggs.—Bramblings, chaffinches, and reed-buntings, which could puncture-eject the artificial egg, normally ejected conspecific eggs with only minor damage to their own eggs (selective ejection). This could be considered to represent grasp ejection. Based on the artificial egg experiments, these three species probably also puncture-ejected the conspecific eggs, despite the fact that the smaller conspecific eggs could have been grasp-ejected. However, ejections of artificial conspecific eggs of sizes similar to natural ones were always by unselective ejection. Of 36 ejections of natural conspecific eggs, 4 ejections resulted in an additional ejection of the hosts' own eggs. This supports the idea that small-billed species such as the Brambling, Common Chaffinch, or Common Reed-Bunting may experience some costs even in puncture-ejecting conspecific eggs. Because Common Cuckoo eggs are both larger and thicker-shelled than the eggs of these three species, the ejection cost is most probably higher when genuine Common Cuckoo eggs are ejected in nature. Northern Orioles, probably the only North American puncture ejectors, damaged some of their own eggs in 13 of 33 observed ejections of Brown-headed Cowbird eggs (Rohwer et al. 1989). Such damage was not as dramatic as that we observed, perhaps because Northern Orioles have greater grasp indices than any of these three species. On the other hand, our observations may support the idea (Davies and Brooke 1988) that some recognition cost is involved in the rejection of a foreign egg. These three species might thus mistakenly have ejected some of their own eggs simply because of recognition problems.

Rejection behavior of cuckoo and cowbird hosts.—More Common Cuckoo than Brown-headed Cowbird hosts were rejectors. As predicted, the frequency of puncture ejectors among cuckoo hosts with grasp indices <200 mm^2 (7/17) was higher than that for cowbird hosts (2/27, $\chi^2 = 7.31$, $P < 0.01$). The number of species eventually found to be puncture ejectors will probably increase as the number of experiments increases (e.g. Reed Warblers; Davies and Brook 1988, 1989).

The Bluethroat and the Spotted Flycatcher, both with grasp indices similar to the Brown-headed Cowbird, must at present be regarded as grasp ejectors. Except for one observation, none of the remaining host eggs in the nest of these two species showed any signs of damage due to puncture ejection. The Common Cuckoo egg was selectively ejected. However, both these species have bills among the longest of all the species with grasp indices of <200 mm^2. Bill length (and strength) may be more important for grasp ejection than the grasp-index value.

The Meadow Pipit accepts Common Cuckoo eggs (Moksnes and Røskaft 1989, Davies and Brooke 1989). The occasional rejection of Common Cuckoo eggs by this species would, based on bill length, presumably take the form of puncture ejection. Our results do not support this prediction. The high rate of desertion could therefore indicate a lack of ability to puncture-eject. However, Davies and Brooke (1989) have made several observations of Meadow Pipits ejecting a Common Cuckoo egg. On the other hand, finches and sparrows might have stronger bills than pipits and wagtails. These stronger bills may make these species more likely to puncture-eject. Our data do not allow any further speculations regarding this point.

We support the prediction that Common Cuckoo hosts with medium-sized bills puncture-eject Common Cuckoo eggs from the nest. The largest potential hosts grasp-ejected, while the smallest hosts deserted their nests. Only a few species deviated from this general rule. Our results verify reports that the percentage of rejection done by ejection increased with bill length of the host (Davies and Brooke 1989). At present we cannot estimate the true cost of puncture ejection, but our observations support the general idea that the greater eggshell-thickness of the North American Brown-headed Cowbirds may have evolved to resist puncture ejection by its smaller-sized host species. Although the thicker eggshell of Common Cuckoos may have evolved for other reasons (Lack 1968), the effect on the host species will be similar to that for Brown-headed Cowbird hosts. That is, Common Cuckoo eggs laid in European host nests should produce reactions similar to those of Brown-headed Cowbird eggs laid in the nests of North American cowbird hosts, if the costs of rejection or acceptance are comparable. For these two groups of hosts, the cost of ejecting the parasitic egg should be similar, relative to respective egg size, shapes, and strength. Nonetheless, the cost to a Common Cuckoo host that accepts a parasitic egg is much higher than for a Brown-headed Cowbird host that accepts a cowbird egg. A Common Cuckoo host should therefore be able to tolerate a higher cost of rejection than a Brown-headed Cowbird host. Furthermore, the cost of puncture ejection should increase as bill size decreases. Selection should favor those Common Cuckoo hosts that puncture-eject the parasitic egg while possessing bills much smaller than those of the American Brown-headed Cowbird hosts.

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