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AN EXPERIMENTAL STUDY OF CO-EVOLUTION BETWEEN THE CUCKOO, *CUCULUS CANORUS*, AND ITS HOSTS.
I. HOST EGG DISCRIMINATION

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SUMMARY

(1) The nests ($n = 711$) of twenty-four species of passerine birds were parasitized experimentally with model cuckoo eggs.

(2) Among current favourite hosts, species for which the cuckoo lays a mimetic egg discriminated against model eggs unlike their own (reed warbler, meadow pipit, pied wagtail), while the dunnock, which is not mimicked, did not discriminate.

(3) Other species, suitable as hosts (invertebrate diet, accessible nests) but rarely used by cuckoos, showed just as much rejection of model eggs unlike their own (chaffinch, blackbird, song thrush), or stronger rejection (spotted flycatcher, reed bunting) than the most strongly rejecting of current favourite hosts.

(4) Two results suggest that the egg discrimination by suitable hosts has evolved in response to cuckoo parasitism. (a) Species unsuitable as hosts (thus with no history of interaction with cuckoos) mainly showed little if any rejection of model eggs unlike their own (seed-eaters—linnet, greenfinch, bullfinch; hole-nesters—great tit, blue tit, pied flycatcher, wheatear). (b) Meadow pipits and white wagtails in Iceland, where they are isolated from cuckoos, showed significantly less discrimination against eggs unlike their own than in Britain, where they are parasitized.

(5) Species with smaller bills suffered greater rejection costs (own eggs damaged) and were more likely to reject model eggs by desertion than species with larger bills, which tended to reject by ejection.

(6) Among species suitable as hosts, there was no tendency for smaller-billed species to reject less. Therefore rejection costs influenced the method of rejection but not rejection frequency.

INTRODUCTION

The cuckoo *Cuculus canorus* L. is a brood parasite, laying its eggs in the nests of various species of passerine birds. There are three main hosts in Britain: meadow pipits *Anthus pratensis* L. in moorland, reed warblers *Acrocephalus scirpaceus* Herman in marshland, and dunnocks *Prunella modularis* L. in woodland and farmland. The pied wagtail *Motacilla alba yarrellii* Gould is another frequently used host (Glue & Morgan 1972; Brooke & Davies 1987). Individual female cuckoos are thought to specialize on one of these hosts (Chance 1940; Baker 1942; Wyllie 1981). The eggs laid by these four cuckoo types, called gentes (singular gens), are distinct and, with the exception of the dunnock gens, mimic the shade and colour of their respective host eggs (Brooke & Davies 1988).

The female cuckoo lays one egg per host nest, usually parasitizing the nest during the host laying period. The cuckoo chick commonly hatches first, whereupon, one by one, it balances the host eggs on its back and ejects them from the nest. Newly hatched host young suffer the same fate and so the cuckoo chick becomes the sole occupant of the nest. It is the cuckoo chick which must do the ejecting, not the female cuckoo when she lays, because hosts desert single eggs but not single chicks (Davies & Brooke 1988). As a result, the host gets no reproductive success from a successfully parasitized nest. Therefore, we expect selection to favour host abilities to decrease cuckoo success. This, in turn, will select for improved trickery by the cuckoo. Co-evolution between brood parasite and host is expected to lead to ever more intricate adaptations and counteradaptations.

We consider three responses by hosts to cuckoo parasitism: (a) rejection of cuckoo eggs, selecting for host egg mimicry by the cuckoo, leading to better discrimination and mimicry; (b) host eggs with distinctive signatures (spot patterns to signify 'this is my egg') selecting for forgery by cuckoos (to indicate 'and so is this'), leading to more distinctive signatures and better forgeries; (c) host discrimination against chicks unlike their own.

We consider these three possible outcomes by comparing egg characteristics and abilities to discriminate eggs and chicks in various species of passerine birds. We compare species suitable as hosts for cuckoos, namely those with nests accessible to a female cuckoo and which feed their young on invertebrate prey (necessary for raising a young cuckoo), with unsuitable species (inaccessible nests or a seed diet) with, therefore, no history of contact with cuckoos. We also compare parasitized populations of two species of favourite cuckoo hosts in Britain with unparasitized populations in Iceland, where there are no cuckoos. Our results show that hosts evolve better egg discrimination in response to cuckoo parasitism (unsuitable hosts and unparasitized populations of suitable hosts are less discriminating), but apparently do not evolve changes in egg patterns or the ability to discriminate chicks. We suggest that the varying degrees of egg discrimination shown among suitable host species represent snap shots in evolutionary time of different stages of a continuing arms race between cuckoos and hosts.

In this paper we consider egg discrimination and defer consideration of the other two responses ((b) and (c) above) and the general discussion to the second paper (Davies & Brooke 1989).

METHODS

Following the procedure pioneered by Rothstein (1975), we behaved as cuckoos ourselves and parasitized the nests of various passerine species with model cuckoo eggs, made from gel coat resin, poured into a mould of Silastic rubber. Two moulds were used, one from a cuckoo egg measuring 23·05 × 17·10 mm and the other from one of 23·70 × 16·95 mm (length × breadth). Both approximate the average dimensions of cuckoo eggs (average of 100 eggs given as 23·05 × 17·23 mm by Witherby *et al.* 1943). The weight of the model eggs (mean of 20 = 3·4 g, range 2·9–3·8) was the same as that of real cuckoo eggs (mean of 31 = 3·4 g, range 2·9–3·8 g; Wyllie 1981). The models were painted with acrylic paints (see Davies & Brooke 1988 for details) to match the colour of four gentes of female cuckoos (Fig. 1).

(i) *Pied wagtail type*: a pale greyish white egg, freckled with grey or brown spots, matching the pale spotted egg of the host.

(ii) *Meadow pipit type*: a brownish-grey egg, spotted and mottled with brown, matching the dark brown egg of the host.

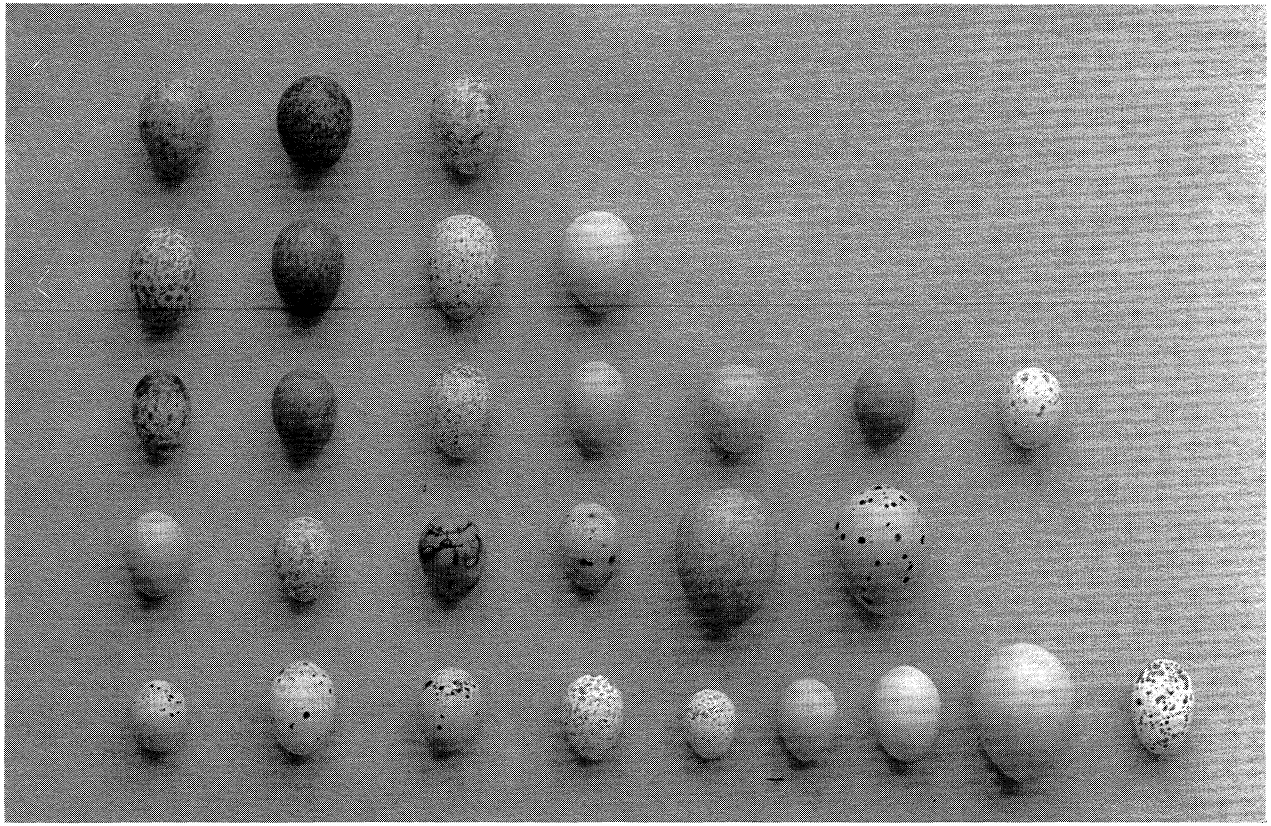

FIG. 1. From left to right: *Top row*: Real cuckoo eggs from reed warbler gens, meadow pipit gens and pied wagtail gens. *Second row*: Model cuckoo eggs representing reed warbler gens, meadow pipit gens, pied wagtail gens, redstart gens. *Third row*: Eggs of current favourite British hosts—reed warbler, meadow pipit, pied wagtail, dunnock, robin, sedge warbler, wren. *Fourth row*: Eggs of species which are suitable but rare hosts—redstart, spotted flycatcher, reed bunting, chaffinch, blackbird, song thrush. *Bottom row*: Eggs of species unsuitable as hosts—linnet, greenfinch, bullfinch, great tit, blue tit, pied flycatcher, wheatear, starling, swallow.

(iii) *Reed warbler type*: a greenish egg, intermediate in darkness between types (i) and (ii) above, with green and brown speckling, matching the greenish eggs of the host (green spotted reed warbler type in Davies & Brooke 1988).

(iv) *Redstart type*: an immaculate pale blue egg, representing a cuckoo gens in Finland which parasitizes the redstart *Phoenicurus phoenicurus* L., mimicking perfectly the colour of the host egg (Wasenius 1936).

Real cuckoos lay their eggs in the afternoon during the host laying period (Chance 1940; Wyllie 1981). To mimic this procedure, our experimental parasitisms were all done in the afternoons (after 12.00 BST), and we tried to find nests before clutch completion. Of a total of 553 nests parasitized, involving twenty-two species, 377 (68·2%) were parasitized during the host laying period or on the day of clutch completion, thirty-five between 1 and 3 days after clutch completion, fifty-four 4 days or more after, and eighty-seven experiments were done on complete clutches of unknown stage of incubation. Most of our experiments, therefore, were done during the period real cuckoos would lay. We show later that the stage of parasitism has no effect on response to model eggs. Real cuckoos remove one, sometimes two host eggs before depositing their own (Chance 1940; Wyllie 1981). We also show later that this has no influence on host response to the models (see also Davies & Brooke 1988) and so, to minimize disturbance to the hosts, we often simply added the model to the clutch or removed a host egg at the time of experimental parasitism and then replaced it on clutch completion.

Model eggs warmed up during incubation and were sufficiently like real cuckoo eggs to fool one experienced ornithologist into recording one as such on a nest record card. Four lines of evidence (see later for details) suggested that small birds also regarded them as real eggs. (i) Species that rejected model eggs unlike their own mostly accepted models that matched their own eggs, thus rejection was not simply a response to the presence of a model per se (e.g. its texture) or a reaction to disturbance by us. (ii) Species that accepted model eggs, whatever their colour, also accepted whole clutches of models. This shows that the bird did not regard the models simply as lumps of resin which would do them no harm and so would be best left in the nest! (iii) Models were rejected in the same way that real cuckoo eggs are rejected. (iv) Accepted models were treated like the host's own eggs; they were moved around the nest during incubation and remained in the nest after the young hatched, like the host's own unhatched eggs.

Experiments with the following species were all done at various sites in Cambridgeshire: reed warbler, dunnock, robin *Erithacus rubecula* L., sedge warbler *Acrocephalus schoenobaenus* L., wren *Troglodytes troglodytes* L., reed bunting *Emberiza schoeniculus* L., chaffinch *Fringilla coelebs* L., blackbird *Turdus merula* L., song thrush *Turdus philomelos* Brehm, linnet *Acanthis cannabina* L., greenfinch *Carduelis chloris* L., bullfinch *Pyrrhula pyrrhula* L. and swallow *Hirundo rustica* L. Experiments with spotted flycatchers *Muscicapa striata* Pallas, great tit *Parus major* L. and starling *Sturnus vulgaris* L. were done in Cambridgeshire and Oxfordshire; blue tits *Parus caeruleus* L. in Oxfordshire; meadow pipits in Derbyshire, Somerset and Cambridgeshire; pied wagtails in Hertfordshire, Cambridgeshire, Surrey, Cumbria, Invernsess-shire, Ross-shire, Tayside and Dyfed; redstart in Cumbria and Dyfed; and pied flycatcher *Ficedula hypoleuca* Pallas and wheatear *Oenanthe oenanthe* L. in Cumbria. There was no indication of any geographical variation in any species' responses to the model eggs.

The experiments were done in 1984–88 and, in any one year, no host territory was used more than once with a given model type. We tried, therefore, to make sure that each experiment done with a particular model type was with a different pair of birds.

RESPONSES OF SPECIES SUITABLE AND UNSUITABLE AS HOSTS

Reactions to model cuckoo eggs

Methods of rejection

We first justify our use of model eggs to test host discrimination. After experimental parasitism, nests were visited at various intervals to check their contents. Model eggs were rejected at 225 nests. Of these, 115 (51·1%) were by ejection, ninety-eight (43·6%) by desertion, three by the building of a new nest on top of the clutch containing the model, and at nine nests involving reed warblers, the hosts were observed pecking the model. In this species pecking was usually followed by desertion (Davies & Brooke 1988) and so in these nine cases we removed the model to minimize disturbance to the birds. Ejected models were sometimes found in vegetation outside the nest rim or on the ground underneath.

Of these four methods of rejection, ejection, building over and pecking were clear responses to the models. Desertion can occur in other circumstances, for example because of disturbance, cold weather or predation of hosts, but we believe that the majority of desertions were rejection responses to the models. Of the seven species that deserted nests containing a model egg unlike their own in colour, all seven showed a lower desertion rate when models like their own eggs were placed in their nests ($P = 0{\cdot}016$, two-tailed sign test). For two species, sample sizes were sufficient to show a significant difference; reed warblers deserted nine out of thirty nests containing a model egg unlike their own compared with none of nineteen containing a mimetic reed warbler type model ($\chi^2 = 5{\cdot}13$, 1 d.f., $P < 0{\cdot}05$), and meadow pipits deserted twenty-five out of fifty-five nests containing an unlike model compared with only four out of twenty-five nests containing a mimetic meadow pipit type model ($\chi^2 = 5{\cdot}24$, 1 d.f., $P < 0{\cdot}05$).

Time to rejection

When models were placed in nests before clutch completion there was often a delay in rejection; in twenty-eight cases the model was known to have been rejected before clutch completion, while in forty-five cases the model was known to have been rejected on or after the day of clutch completion. This delay may arise simply because hosts do not inspect their clutches closely until they are complete and incubation begins in earnest. Models put in before clutch completion took significantly longer to be rejected (forty-nine known to be rejected within 3 days, twenty-nine known to be rejected after more than 3 days) than models put in on the day of clutch completion or later (seventy-four known to be rejected within 3 days, only five after more than 3 days; $\chi^2 = 20{\cdot}23$, 1 d.f., $P < 0{\cdot}001$). Delayed rejection until clutch completion also often occurs in response to real cuckoo eggs (Gärtner 1982) and may be adaptive if it is easier to spot an odd egg once the clutch is complete (Davies & Brooke 1988).

Once the clutch was complete, most rejections took place within 3 days. For models put in before clutch completion, sixty-eight were known to have been rejected within 3 days of clutch completion and only thirteen more than 3 days after clutch completion. For models put in on the day of clutch completion or later, seventy-four were known to have been rejected within 3 days and only five after an interval of more than 3 days, a similar proportion ($\chi^2 = 2{\cdot}87$, 1 d.f., N.S.). Thus, including models put in at all stages, for which the time of rejection was accurately known, 142 out of 160 (88·8%) were rejected within 3 days of clutch completion or experimental parasitism, whichever was the later.

TABLE 1. Rejection frequencies of model eggs unlike the host's own eggs, comparing cases where the model was put in the host nest during the laying period (when real cuckoos lay) with cases where the model was put in later, after the day of clutch completion. There was no significant difference between treatments (i) and (ii), or (i) and (iii), for any species

	No. nests where an unlike model egg was rejected when model put in		
	During laying period or day clutch completed (i)	After day of clutch completion* (ii)	(iii)
Species			
Reed warbler	27/43	1/6	7/12
Meadow pipit	8/11	8/17	20/47
Pied wagtail	11/14	3/9	16/24
Blackbird	10/21	9/11	11/13
Song thrush	16/30	8/11	8/11

* (ii) Excludes experiments done on complete clutches of unknown stage of incubation. (iii) Includes these unknown cases, which are more likely to be in this category than in (i).

Not all nests were checked at 3 days after clutch completion and so we used the following criterion for rejection: 'nests where the model egg could have been rejected within 3 days of clutch completion or experimental parasitism, whichever was the later'. Only seven of the 115 ejections and eleven of the ninety-eight desertions definitely occurred after this criterion ($\chi^2 = 1{\cdot}20$, 1 d.f., N.S.). Including all four methods of rejection, 207 of the 225 rejections (92%) occurred within the criterion. Models still in attended nests after the criterion were regarded as 'accepted' by the birds. Nests that hatched or suffered predation within 3 days of model insertion were not scored. In only thirty-two of a total of 585 experiments (5·5%) was the clutch depredated before our 3-day criterion. Predation could cause a bias in the measure of acceptance rates (see Davies & Brooke 1988 for discussion), but because predation before our criterion was rare and because there was no significant difference in predation rate between species, this potential problem did not arise.

Effects of stage of parasitism and host egg removal

There was no significant difference in the rejection rate of models put in during the host laying period or on the day of clutch completion (when real cuckoos lay) compared with models put in at a later stage (Table 1). This result was further supported by experiments with blackbirds and song thrushes who had previously ejected models put in their nests during the laying period. When parasitized with the same model type a second time in late incubation (7 days or more after clutch completion), three out of the five blackbirds and seven out of the eight song thrushes ejected the model again. In the analysis which follows we have therefore included experiments done at all stages, though most were done during the host laying period (see Methods).

Table 2 shows that host egg removal had no influence on the rejection rates of our model eggs. In the analysis below we have therefore combined the results of all experiments, including those where we removed a host egg with those where we did not.

TABLE 2. Rejection frequencies of model eggs, comparing cases where a host egg was removed (which is what real cuckoos do) with cases where no host egg was removed. There are no significant differences

	No. nests where model egg was rejected			
	Model unlike host eggs		Model like host eggs	
	Host egg removed?		Host egg removed?	
Species	Yes	No	Yes	No
Reed warbler	16/26	13/22	0/7	0/11
Meadow pipit	4/11	24/47	1/4	5/23
Dunnock	1/16	0/9	0/3	0/2
Robin	4/14	1/11	—	—
Spotted flycatcher	4/5	3/3	1/1	0/4
Blackbird	2/2	4/7	2/6	2/10
Song thrush	3/5	8/11	0/3	0/3

Responses to the four types of model cuckoo eggs

Table 3 summarizes experiments done with the four model types for twenty-two species.

Current favourite cuckoo hosts

Reed warblers showed significant variation in response to the four model types ($\chi^2 = 27{\cdot}05$, 3 d.f., $P < 0{\cdot}001$). They were more likely to accept mimetic reed warbler-type models than meadow pipit-type models ($P < 0{\cdot}05$), pied wagtail-type models ($P < 0{\cdot}001$) and redstart-type models ($P < 0{\cdot}001$). There was no significant variation in response to the three non-mimetic models ($\chi^2 = 5{\cdot}59$, 2 d.f., N.S.). Meadow pipits also showed significant variation in response to the four model types ($\chi^2 = 18{\cdot}90$, 3 d.f., $P < 0{\cdot}001$). The mimetic meadow pipit-type model was most accepted , but in pairwise comparisons with the three non-mimetic models, the only significant difference was with redstart-type models ($P < 0{\cdot}001$). Considering only the three non-mimetic models, there was still significant variation in response ($\chi^2 = 13{\cdot}09$, 2 d.f., $P < 0{\cdot}01$) due to greater rejection of redstart-type models than of reed warbler type ($P < 0{\cdot}01$) and pied wagtail type ($P < 0{\cdot}01$). For pied wagtails, there was no significant variation in response to the four model types, though the mimetic pied wagtail type was the model most accepted.

By contrast, dunnocks accepted all four model types. Dunnocks have pure pale blue eggs but despite the striking differences in coloration and the presence of spots, pied wagtail, reed warbler and meadow pipit-type cuckoo eggs (with one exception) were all accepted, as were the blue redstart-type models similar in coloration to the dunnock's own eggs. If dunnocks had poor colour vision or found it difficult to detect egg colour in their nests, which are built in dense cover, then it is possible that their own blue eggs appeared greyish in colour and the various models also appeared grey, thus matching in shade. We did further experiments with white models and black models, which should have been easily detected as different in shade. All four black models were accepted as were four of five white models (one was deserted). Both reed warblers (Davies & Brooke 1988) and meadow pipits (Moksnes & Røskaft 1989) are more likely to reject a model cuckoo egg if they have seen a stuffed cuckoo on their nest, but even this treatment did not stimulate dunnocks to reject. At eight nests we placed a stuffed cuckoo on the nest for 10 min. The

TABLE 3. Rejection frequencies of four types of model cuckoo egg by twenty-two host species. See Fig. 1 for photographs of model eggs and host eggs

	No. of nests where model egg was rejected					
Species	Redstart type	Pied wagtail type	Reed warbler type	Meadow pipit type	All models unlike host eggs (excluding *) (%)	
(a) Current cuckoo hosts						
1. Reed warbler	17/28	13/16	0/19*	4/11	34/55	(61·8)
2. Meadow pipit	15/18	9/25	4/15	6/27*	28/58	(48·3)
3. Pied wagtail	10/13	7/14*	5/7	12/18	27/38	(71·0)
4. Dunnock	0/5*	0/7	0/4	1/6	1/17	(5·9)
5. Robin	1/7	2/7	—	2/11	5/25	(20·0)
6. Sedge warbler	0/2	1/2	—	0/1	1/5	(20·0)
7. Wren	—	—	—	0/5	0/5	(0·0)
(b) Suitable but rare hosts						
8. Redstart	0/1*	2/4	—	0/4	2/8	(25·0)
9. Spotted flycatcher	3/3	2/3	—	3/3	8/9	(88·9)
10. Reed bunting	3/3	3/3	—	3/3	9/9	(100·0)
11. Chaffinch	1/2	6/6	0/2	2/5	9/15	(60·0)
12. Blackbird	13/22	5/7	3/5	—	21/34	(61·8)
13. Song thrush	3/11	3/5	6/6	12/19	24/41	(58·5)
(c) Unsuitable as hosts						
14. Linnet	0/4	0/5	—	0/5	0/14	(0·0)
15. Greenfinch	0/3	0/4	—	0/5	0/12	(0·0)
16. Bullfinch	—	0/1	—	0/7	0/8	(0·0)
17. Great tit	1/3	0/3	1/3	0/3	2/12	(16·7)
18. Blue tit	0/3	0/3	0/3	0/3	0/12	(0·0)
19. Pied flycatcher	1/5*	0/5	—	0/5	0/10	(0·0)
20. Wheatear	—*	0/5	0/3	1/5	1/13	(7·7)
21. Starling	1/2*	1/2	—	3/5	4/7	(57·1)
22. Swallow	0/3	0/1	—	0/4	0/8	(0·0)

* Indicates model eggs which were like the host's own eggs.

dunnocks approached and showed alarm in all cases. We then placed a meadow pipit-type model in the nest; it was accepted in all eight cases.

These results suggest that dunnocks do not discriminate against unlike eggs, but an alternative explanation is that they are showing even finer discrimination than reed warblers and meadow pipits; perhaps the dunnocks realized that the eggs were only models, which would result in little cost, and so decided to accept them! To test this, we replaced the dunnock's own eggs one at a time during laying with model eggs. The model clutch was left in the nest for 2 days after clutch completion and then replaced with the dunnock's own clutch. In one case, with pied wagtail-type models, the dunnock deserted once the clutch was completed. In three other cases, however, the model clutch was incubated (clutches of four reed warbler-type, four pied wagtail-type and four redstart-type models), and the dunnocks also accepted their own eggs back and continued incubation. This result supports the idea that dunnocks regarded the models as real eggs and simply showed no discrimination with respect to colour and spot pattern.

Some species are known to reject like eggs (those of conspecifics) before laying, but to accept them once laying has begun (Vehrencamp 1977; Mumme, Koenig & Pitelka 1983; Emlen & Wrege 1986; Møller 1987; Stouffer, Kennedy & Power 1987). As a final attempt to induce dunnocks to show rejection, we placed models in completed nests before laying had begun. One out of four redstart-type models was ejected and one of five meadow pipit models was ejected. These were the only ejections recorded in a total of forty-eight experiments where a model egg was placed in a dunnock nest.

Robins showed some rejection (Table 3), but most of the models were accepted and there was no significant variation in response to different types. None of the models matched the robin's own eggs closely. Too few experiments were done with sedge warblers and wrens to merit detailed comments.

These results with the current favourite cuckoo hosts suggest that host discrimination is the main selective agent responsible for the type of eggs laid by cuckoos in the various gentes in Britain (Brooke & Davies 1988). Cuckoos specializing on reed warblers, meadow pipits and pied wagtails each lay a mimetic egg and the experiments showed that all three species discriminate against badly matching eggs. In all three cases, the model most accepted was the one resembling the mimetic egg laid by the appropriate gens of cuckoo. However, convincing discrimination in favour of mimetic eggs over all three other types was shown only by reed warblers. By contrast, dunnock-cuckoos do not lay a mimetic egg as expected from the fact that this host shows no discrimination. On average robin-cuckoo eggs are no different in shade from those laid by pied wagtail-cuckoos and cuckoo eggs in robin nests are significantly more variable in shade than those of the other gentes. These findings suggest that robin-cuckoo eggs are not distinct (Brooke & Davies 1988). The degree of mimicry is not strong, as expected from the lack of strong discrimination shown to the model eggs.

Other species

There are insufficient data to do a statistical comparison for any of the other species' response to all four model types. The most striking result was that some tended to accept all the model types (e.g. greenfinch, linnet, great tit, blue tit, pied flycatcher, swallow) whereas others tended to reject them, irrespective of type (spotted flycatcher, reed bunting).

For four species which rejected models unlike their own eggs, we painted models to mimic their own eggs in colour and spot pattern. Blackbirds rejected mimetic cuckoo eggs at only five out of twenty-two nests compared with twenty-one out of thirty-four rejections of unlike eggs (the total in Table 3; $P < 0{\cdot}01$). Song thrushes also showed less rejection of mimetic eggs (only one out of seven rejected) than of unlike eggs (twenty-four out of forty-one in Table 3; $P < 0{\cdot}10$). These results show that the rejection of unlike models by these two large species was not simply because the model cuckoo egg was much smaller than their own eggs (Fig. 1). Spotted flycatchers rejected only one out of five mimetic models compared with eight out of nine unlike models ($P < 0{\cdot}05$). Chaffinches, however, showed no difference in response: eight out of fourteen mimetic eggs rejected compared with nine out of fifteen unlike models. In total, all ten species tested with both mimetic and non-mimetic models, which showed some rejection of model eggs unlike their own, showed less rejection of mimetic models (two-tailed sign test, $P < 0{\cdot}002$).

As with the dunnock, we asked whether the accepting species regarded the models as real eggs. To test this, for three accepter species (linnet, bullfinch, greenfinch) we replaced eggs as they were laid with meadow pipit-type models, left the birds with a complete model clutch for 2 days and then replaced the models with the bird's own clutch. At seven out of nine nests the clutch of models was incubated and incubation continued when it was replaced with the species' own eggs (three out of three linnets, one out of one bullfinch,

TABLE 4. Methods used by hosts to reject model eggs

Species	No. cases model egg rejected		
	By ejection	By desertion	Other
Reed warbler	16	7	11*
Meadow pipit	5	29	—
Pied wagtail	12	21	1†
Dunnock	—	2	—
Robin	2	3	—
Sedge warbler	—	1	—
Spotted flycatcher	9	—	—
Reed bunting	1	8	—
Chaffinch	11	6	—
Blackbird	22	4	—
Song thrush	22	3	—
Great tit	—	2	—
Pied flycatcher	—	1	—
Starling	5	—	—
Redstart	2	—	—
Wheatear	1	—	—

* +2 built over; 9 pecking observed at model.
† Built over.
Note: Total rejections for unlike and like models, as in Table 3 and text.

three out of five greenfinches; two greenfinches deserted after clutch completion). The fact that whole clutches of models were largely accepted, as with dunnocks, suggests that the model eggs were regarded as real. Furthermore, although linnets and greenfinches accepted all the models in Table 3, when a meadow pipit model was put in complete nests before laying, six out of six linnets rejected the model (five built over, one deserted) and two out of seven greenfinches rejected (one deserted, one built over). 'Building over' represented a clear rejection of the model because it involved adding a great excess of lining to the nest. The fact that accepter species rejected models in contexts where other species reject conspecific eggs (i.e. before laying—see above) again supports the idea that the models were regarded as real eggs.

Species differences in method of rejection

The method of rejection varied significantly across species (Table 4). For the ten species with five or more rejections, there was significant variation in the proportions ejected *v.* deserted and built over ($\chi^2 = 68{\cdot}43$, 9 d.f., $P < 0{\cdot}001$; reed warbler rejection by pecking is omitted from this analysis). Species with smaller bills were more likely to reject by desertion and species with larger bills by ejection (Fig. 2). The most likely explanation for this correlation is simply that small-billed birds find it more difficult to eject the model and so desert instead. One of the costs of trying to eject a model egg, or a real cuckoo egg, is that of cracking one or more own eggs (Davies & Brooke 1988). The three largest species tested showed no disappearance of own eggs accompanying ejection of models (blackbird none out of twenty-two; song thrush none out of twenty-two; starling none out of five). Smaller species, however, did show apparent ejection costs (reed warbler, seven of sixteen ejections accompanied by one or more own eggs disappearing; chaffinch, two out of eleven; reed bunting one out of one). Evidence that these own egg disappearances

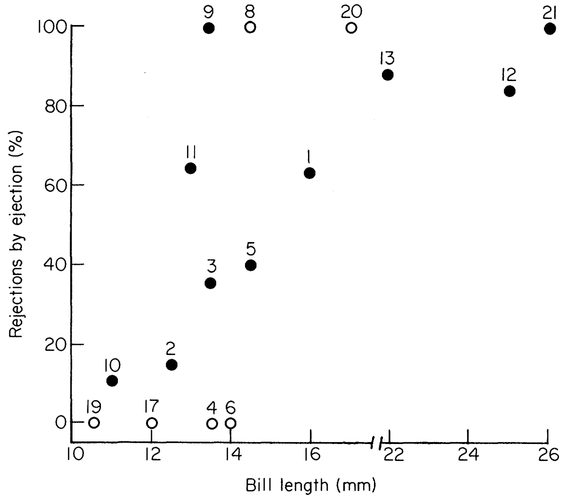

FIG. 2. Correlation between bill length (from Witherby *et al.* 1943) and the percentage of rejections of model eggs (like and unlike) which were by ejection. Models not ejected were rejected by desertion or building over (pecking omitted from this analysis). Considering all sixteen species which showed some rejection, Spearman rank correlation, $r_s = 0{\cdot}684$; $P < 0{\cdot}01$. For the ten species with five or more rejections (solid symbols), $r_s = 0{\cdot}706$; $P < 0{\cdot}05$. For key to species see Table 3.

accompanied ejection of the model is provided by reed warblers, where one or more own eggs were significantly more likely to disappear from nests where models had been ejected (seven out of sixteen) than in nests where models were accepted (only one out of forty; $\chi^2 = 12{\cdot}69$, 1 d.f., $P < 0{\cdot}001$). If small-billed species suffered very high ejection costs or were simply unable to eject the model, then desertion may have been the best way to reject.

Although the models were solid, unlike real cuckoo eggs, and therefore could not be picked up by puncturing, there was no evidence that this resulted in different treatment compared with real cuckoo eggs. For example, reed warblers tend to reject real cuckoo eggs by ejection, while meadow pipits tend to reject by desertion (Peter Davis, personal communication), the same difference observed in response to models (Table 4).

Hypotheses for species differences in response to unlike model eggs

In general, with the exception of greater acceptance of mimetic eggs, there was little variation within a species in rejection rate of the different model types. Therefore, in order to compare the responses of different species, we have lumped the data for unlike models of the various types (final column, Table 3). Considering all twenty-two species tested, there was significant variation in the proportion of unlike model eggs rejected ($P < 0{\cdot}001$). We consider three hypotheses to explain these marked differences, summarized in Fig. 3.

(1) *History of contact with cuckoos*

The species in Table 3 have been divided a priori into three categories. The first two ((a) and (b)) include current favourite cuckoo hosts and suitable but rare hosts. All these species have open nests, accessible for parasitism by cuckoos, and all feed their young on invertebrate prey, probably necessary for raising a cuckoo chick. The third category (c) is

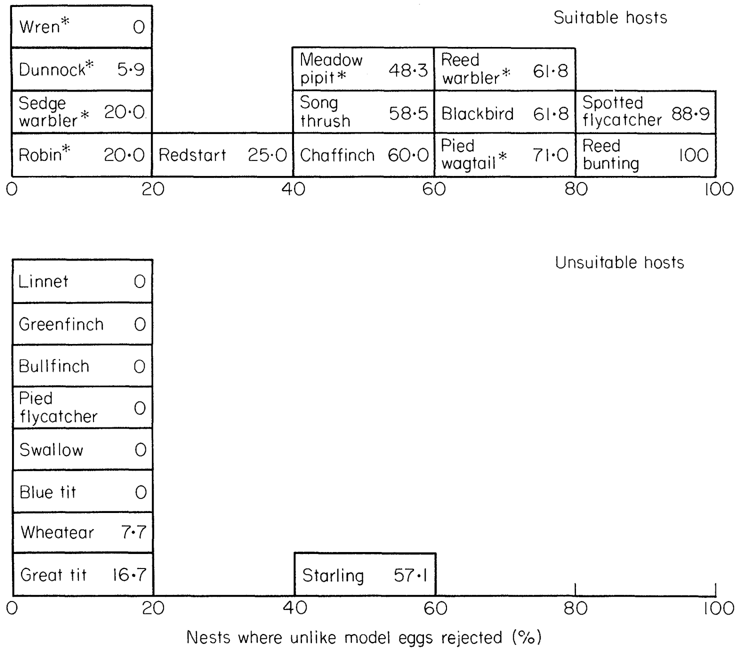

FIG. 3. Percentage of nests where model eggs unlike the host's own eggs were rejected. Species suitable as cuckoo hosts show varying degrees of rejection (top), while species that are unsuitable show largely no rejection (bottom). Within suitable species, some rarely used hosts show stronger rejection than the most commonly used hosts (starred). Data taken from Table 3.

unsuitable as hosts for cuckoos for various reasons. Linnet, greenfinch and bullfinch have open nests but all feed their young largely on seeds; great tit, blue tit, pied flycatcher, wheatear and starling feed their young on invertebrates but nest in holes inaccessible to a female cuckoo; swallows have accessible nests and a suitable diet, but they feed their young by regurgitating a bolus of food from a throat pouch, a method probably not suited for feeding a young cuckoo—all cuckoo hosts provision by carrying food in the bill.

The most striking result in Table 3 is that the suitable hosts (thirteen species in (a) and (b)) are significantly more discriminating against model eggs unlike their own than unsuitable species (nine species in (c); Mann–Whitney U-test, two-tailed, $P<0{\cdot}002$; Fig. 3). Suitable hosts showed varying degrees of rejection, but among the unsuitable species six out of the nine showed no rejection at all, and only the starling showed signs of strong rejection. The fact that unsuitable species, with presumably no history of interaction with cuckoos, show largely no rejection of unlike eggs suggests that rejection evolves mainly in response to parasitism by cuckoos.

The second interesting feature of the results in Table 3 and Fig. 3 is that among suitable hosts ((a) and (b)) there is still significant variation in the proportion of unlike model eggs rejected (omitting the two species with only five experiments, $\chi^2=50{\cdot}31$, 10 d.f., $P<0{\cdot}001$). There is a trend for the current favourite hosts (seven species in (a)) to be less discriminating against unlike eggs than rarely used hosts (six species in (b); Mann–Whitney U-test, two-tailed, $P=0{\cdot}074$). If, as the comparison with unsuitable hosts suggests, rejection evolves in response to cuckoos, this result raises the intriguing possibility that suitable species now rarely used were former victims which evolved strong

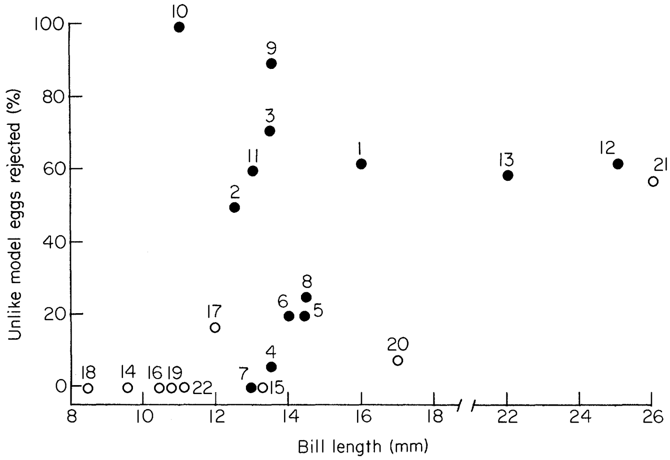

FIG. 4. Correlation between bill length (from Witherby *et al.* 1943) and the percentage of rejection of unlike model eggs. Open circles are species unsuitable as cuckoo hosts; solid circles are suitable host species. (Spearman rank correlation, $r_s = 0{\cdot}533$; $P < 0{\cdot}01$; $n = 22$.) However, among suitable host species only, the correlation is not significant ($r_s = -0{\cdot}043$; $n = 13$). Key to species see Table 3.

rejection and so forced the cuckoo to turn to new hosts (see paper II, Davies & Brooke 1989).

The comparisons above, between the three categories of hosts in Table 3, have regarded each species as an independent sample. In some comparative studies this may not be justified (Clutton-Brock & Harvey 1979), but there are two reasons for thinking it is reasonable in this case. First, the time over which rejection evolves is much shorter than that for the evolution of species differences (see Discussion, paper II). Second, species that accepted most of the unlike models ($\leqslant 20\%$ rejected) occurred in seven of the eleven subfamilies in Table 3, and rejecter species ($> 20\%$ rejection) in seven subfamilies, with three subfamilies having both rejecter and accepter species. Of the two species tested in the tribe Muscicapini, the open-nesting spotted flycatcher (a suitable host) was a strong rejecter of unlike eggs while the hole-nesting pied flycatcher (inaccessible to cuckoos) showed no rejection at all. Of the four species tested in the finch family, Fringillidae, the one species that feeds its young predominantly on invertebrates, and is therefore suitable as a cuckoo host (the chaffinch), showed strong rejection, while all three unsuitable hosts, which feed their young mostly on seeds (greenfinch, linnet, bullfinch) showed no rejection. These results indicate that rejection is not constrained by taxonomy but rather evolves whenever a species is likely to have been exploited by cuckoos.

(2) *Costs of rejection*

Species with small bills were more likely to accept unlike model eggs (Fig. 4). However, this correlation arose simply because there were more small-billed species among the unsuitable hosts. Within suitable hosts there was no significant correlation between bill length and rejection rate (Fig. 4). There was no correlation between method of rejection (percentage rejections by desertion) and overall rejection rate (percentage unlike models rejected; for all fifteen species which showed some rejection of unlike models, Spearman rank correlation, $r_s = -0{\cdot}209$, N.S.; for the ten species with five or more rejections,

$r_s = 0{\cdot}085$, N.S.). Thus there was no indication that species with a more costly method of rejection (desertion) were less likely to reject.

These results contrast with those of Rohwer & Spaw (1988) for hosts of the cowbird *Molothrus ater*, where small-billed species were more likely to accept parasitic eggs. They suggest that small-billed hosts may be unable to puncture the cowbird's thick-shelled egg and that acceptance may be better than desertion because the host often rears some of its own young along with the parasite. For cuckoo hosts, however, there is no reproductive success to be gained from acceptance of a cuckoo egg because the young cuckoo always ejects the host eggs or young; this may explain why small-billed hosts of this parasite are willing to sustain the greater rejection costs of desertion.

(3) *Intraspecific brood parasitism*

In a number of species, some females lay eggs in the nests of conspecifics (Yom Tov 1980; Andersson 1984). This could provide a selective pressure for the evolution of egg discrimination. It is tempting to invoke this as an explanation for the rejection shown by the one unsuitable cuckoo host, the starling, a species known to have high frequencies of intraspecific egg parasitism (Andersson 1984). However, there are two reasons for concluding that this is not a major selective pressure explaining the species differences in Table 3. First, it would be remarkable if the species unsuitable for cuckoos were also the ones which had the least intraspecific brood parasitism, which would be necessary for this hypothesis to explain the striking difference in rejection rates between species in category (c) in Table 3 and the rest. In fact, apart from the starling, one other species in (c), the swallow, is also known to have high frequencies of brood parasitism by conspecifics (Møller 1987).

Second, given that relatively crude mimetic models were accepted by most species (see above), it seems unlikely that own egg recognition is sufficiently good to reject the eggs of conspecifics. To examine this, we swopped a single egg between clutches to test for discrimination in two species which showed strong rejection of unlike models. A conspecific's egg was accepted in all ten chaffinch nests and all four reed warbler nests. Although some species reject conspecific eggs (Victoria 1972; Bertram 1979), many species which are known to have frequent intraspecific brood parasitism do not discriminate against other females' eggs when placed in among a clutch of their own (Brown 1984; Emlen & Wrege 1986; Stouffer, Kennedy & Power 1987; Møller 1987).

EXPERIMENTS IN ICELAND ON HOST POPULATIONS ISOLATED FROM CUCKOOS

The best explanation of the species' differences in Table 3 is clearly the first hypothesis, namely that egg rejection evolves largely as a response to parasitism by cuckoos. If this is true, then we would predict that in the past, before current favourite hosts were parasitized, they would have shown no discrimination against unlike eggs, just like the unsuitable hosts which have never engaged in an arms race with the cuckoo. A direct test of this prediction is clearly impossible but an equivalent experiment can be done.

The cuckoo breeds across the Palearctic region, from western Europe to Japan (Cramp & Simmons 1985), but it is absent from Iceland, where it is only a rare vagrant and has never been known to breed (Skarphedinsson 1982). Iceland does, however, have breeding

TABLE 5. Rejection frequencies of model cuckoo eggs by meadow pipits and pied/white wagtails in parasitized populations (Britain) and unparasitized populations isolated from cuckoos (Iceland)

	No. nests where model rejected		
Species; model type	Britain (parasitized)	Iceland (unparasitized)	Significance of difference
Meadow pipit, *Anthus pratensis*			
Pied wagtail type	9/25	0/13	$P<0{\cdot}05$
Reed warbler type	4/15	1/3	N.S.
Redstart type	15/18	4/11	$P<0{\cdot}05$
Pied/White wagtail, *Motacilla alba*			
Meadow pipit type	12/18	0/15	$P<0{\cdot}001$
Reed warbler type	5/7	0/3	$P=0{\cdot}083$*
Redstart type	10/13	5/10	N.S.

* Fisher exact probability test; other tests refer to χ^2, 1 d.f.

populations of meadow pipits and white wagtails (*Motacilla alba alba* L.). These species are both common hosts of the cuckoo in Britain (the pied wagtail *M. alba yarrellii* is the British subspecies of the white wagtail), and both show strong rejection of unlike eggs which has selected for egg mimicry by their respective cuckoo gentes (see above and Brooke & Davies 1988). Meadow pipits are also common hosts of the cuckoo in Scandanavia (Moksnes & Røskaft 1987) and white wagtails are common hosts in both Finland (Wasenius 1936) and central Europe (Löhrl 1979). As in Britain, on continental Europe both cuckoo gentes lay a mimetic egg.

Assuming the Icelandic pipit and wagtail populations are isolated from the parasitized populations in other parts of Europe (see below) we predicted that, because they have no known history of contact with cuckoos, they would show no discrimination against cuckoo eggs. We spent 5 weeks during May and June 1987 at Myvatn in north Iceland. Some experiments were also done by Philip Whitfield in Melrakasetta, north-east Iceland, in 1986 and 1987. As in the previous experiments, all nests were parasitized with model eggs in the afternoon when there were host eggs in the nest, mainly during laying or early incubation. No host eggs were removed. The same criterion as before was used to score acceptance. All rejections, either by ejection or desertion, occurred within 3 days of model insertion.

In Iceland, both meadow pipits and white/pied wagtails showed less discrimination of model cuckoo eggs unlike their own than in Britain (Table 5). In Britain, both species rejected models painted to represent the eggs of the other species' cuckoo gens; in Iceland all these models were accepted even though they were clearly different from the host's own eggs (Fig. 1). These results support the conclusion from the comparative data (Table 3) that host discrimination has evolved in response to parasitism by cuckoos.

Against our prediction of no rejection, however, was the rejection shown by both Icelandic pipits and wagtails to the blue redstart-type models (Table 5). Meadow pipits rejected three redstart models by desertion and one by ejection; wagtails rejected four by ejection and one by desertion. For both species the rejection frequencies were lower than in Britain, but the difference was significant only for meadow pipits.

We did model egg experiments with two other Icelandic passerines. Snow buntings *Plectrophenax nivalis* L. accepted model eggs at all six nests tested (one redstart-type model, one wagtail-type model, three pipit-type models and one reed warbler-type model, none of which closely resembled the host eggs). Redwings *Turdus iliacus coburni* Sharpe rejected a wagtail-type model at one out of ten nests, a meadow pipit-type model at one out of ten nests and redstart-type models at seven out of ten nests (eight ejections, one desertion). Arnason (1985) also showed that redwings reject blue model eggs. The rejection rate of wagtail-type models was significantly less than that shown by the blackbird in Britain (Table 3; $P < 0{\cdot}05$), a congener which has very similar eggs to the redwing. This provides further support for the idea that finer egg discrimination evolves in species exposed to cuckoo parasitism. However, as with the pipits and wagtails, the rejection of redstart models was not expected. If egg discrimination evolves only in response to cuckoo parasitism, then Icelandic populations should have accepted all the models, like seed-eating and hole-nesting species in Britain.

We consider three hypotheses to explain the discrimination shown by the Icelandic birds, assuming our interpretation of the comparative data in Table 3 is correct, that discrimination evolves primarily in response to cuckoo parasitism.

(1) Cuckoos may have formerly nested in Iceland, before the arrival of the Vikings and their livestock (874 AD) which led to the devastation of the birch forest and, perhaps, a reduced avifauna (Einarsson 1968).

(2) The post-glacial founders of present-day Icelandic passerine populations would not have colonized more than about 9000 years ago (Einarsson 1968). If these populations were derived from parasitized populations in other parts of Europe, they may still have some legacy of discrimination inherited from their ancestors. Egg discrimination would presumably wane slowly because, although of no advantage in the absence of cuckoos, it would impose only a small cost, that of occasionally discriminating against an aberrant egg of one's own.

(3) There may be some gene flow between Icelandic populations and the parasitized populations in other parts of Europe. Ringing recoveries have shown that Icelandic pipits, wagtails and redwings mix with other European populations in winter, when they migrate to south-west Europe (Skarphedinsson 1982). However, at least for redwings, the interchange must be very limited because Icelandic populations are sufficiently distinct

TABLE 6. Measurements of Icelandic populations of male pied/white wagtails and male meadow pipits (made in Reykjavik, Museum of Natural History) compared with British populations (measured at British Museum, Tring)

	Mean ± S.E., length mm (*n*)		
	Britain		Iceland
Pied/White wagtail, *Motacilla alba*			
Wing	88·4 ± 0·3 (50)		88·3 ± 0·4 (24)
Bill	15·3 ± 0·1 (49)	***	13·3 ± 0·1 (24)
Tarsus	23·6 ± 0·1 (50)	*	22·9 ± 0·2 (23)
Meadow pipit, *Anthus pratensis*			
Wing	79·9 ± 0·3 (38)	*	81·0 ± 0·3 (51)
Bill	14·2 ± 0·1 (37)	***	12·5 ± 0·1 (51)
Tarsus	21·2 ± 0·1 (37)		21·1 ± 0·1 (48)

t-test, two-tailed. $^{*}P < 0{\cdot}02$, $^{***}P < 0{\cdot}001$.

morphologically to be designated as a separate sub-species, *Turdus iliacus coburni*. British pied wagtails *M. a. yarrellii* are also morphologically distinct and designated a different sub-species from the Icelandic wagtail *M. a. alba*.

We analysed the Icelandic ringing recoveries for pipits and wagtails and these provided no evidence for mixing between breeding populations. All recoveries in other parts of Europe of young birds ringed as nestlings in Iceland were in the winter, August–April ($n = 18$ for wagtails, $n = 15$ for pipits). All foreign recoveries of adults ringed in Iceland in the breeding season were also in the winter ($n = 5$ for wagtails, $n = 11$ for pipits). All birds found in Iceland in the breeding season which had been ringed in other parts of Europe, had been ringed in the winter ($n = 8$ for wagtails; $n = 3$ for pipits). All these recoveries, therefore, are consistent with the view that Icelandic birds migrate to south-west Europe for the winter and then return to Iceland to breed. Measurements of Icelandic pipits and wagtails also showed differences from British populations which may reflect genetic differences (Table 6). We recognize, however, the difficulty of detecting the limited amount of gene flow which may result in some discrimination being 'inserted' into Icelandic populations.

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REFERENCES

Andersson, M. (1984). Brood parasitism within species. *Producers and Scroungers: Strategies of Exploitation and Parasitism* (Ed. by C. J. Barnard), pp. 195–228. Croom Helm, London.

Arnason, Th. (1985). *Hafnar skógarthrösturinn* (Turdus iliacus coburni) *framandi eggi i hreidri sinu?* (Does the redwing reject a foreign egg in its nest?) Unpublished B.S. thesis, University of Reykjavik, Iceland.

Baker, E. C. S. (1942). *Cuckoo Problems*. Witherby, London.

Bertram, B. C. R. (1979). Ostriches recognize their own eggs and discard others. *Nature*, **279**, 233–234.

Brooke, M. de L. & Davies, N. B. (1987). Recent changes in host usage by cuckoos *Cuculus canorus* in Britain. *Journal of Animal Ecology*, **56**, 873–883.

Brooke, M. de L. & Davies, N. B. (1988). Egg mimicry by cuckoos *Cuculus canorus* in relation to discrimination by hosts. *Nature*, **335**, 630–632.

Brown, C. R. (1984). Laying eggs in a neighbour's nest: benefit and cost of colonial nesting in swallows. *Science*, **234**, 83–85.

Chance, E. P. (1940). *The Truth about the Cuckoo*. Country Life, London.

Clutton-Brock, T. H. & Harvey, P. H. (1979). Comparison and adaptation. *Proceedings of the Royal Society of London*, B, **205**, 547–565.

Cramp, S. & Simmons, K. E. L. (Eds) **(1985).** *Handbook of the Birds of Europe, the Middle East and North Africa*, Vol. 4. Oxford University Press, Oxford.

Davies, N. B. & Brooke, M. de L. (1988). Cuckoos versus reed warblers: adaptations and counteradaptations. *Animal Behaviour*, **36**, 262–284.

Davies, N. B. & Brooke, M. de L. (1989). An experimental study of co-evolution between the cuckoo, *Cuculus canorus*, and its hosts. II. Host egg markings, chick discrimination and general discussion. *Journal of Animal Ecology*, **58**, 225–236.

Einarsson, Th. (1968). *Jardfraedi.* Mal og Menning, Reykjavik.

Emlen, S. T. & Wrege, P. H. (1986). Forced copulations and intra-specific parasitism; two costs of social living in the white-fronted bee-eater. *Ethology*, **71,** 2–29.

Gärtner, K. (1982). Zur Ablehnung von Eiern und Jungen des Kuckucks (*Cuculus canorus*) durch die Wirtsvögel: Beobachtungen und experimentelle Untersuchungen am Sumpfrohrsänger. *Die Vogelwelt*, **103,** 201–224.

Glue, D. & Morgan, R. (1972). Cuckoo hosts in British habitats. *Bird Study*, **19,** 187–192.

Löhrl, H. (1979). Untersuchungen am Kuckuck *Cuculus canorus* (Biologie, Ethologie und Morphologie). *Journal für Ornithologie*, **120,** 139–173.

Moksnes, A. & Røskaft, E. (1987). Cuckoo host interactions in Norwegian mountain areas. *Ornis Scandanavica*, **18,** 168–172.

Moksnes, A. & Røskaft, E. (1989). Adaptations of meadow pipits to parasitism by the common cuckoo. *Behavioural Ecology and Sociobiology* (in press).

Møller, A. P. (1987). Intraspecific nest parasitism and antiparasite behaviour in swallows, *Hirundo rustica. Animal Behaviour*, **35,** 247–254.

Mumme, R. L., Koenig, W. D. & Pitelka, F. A. (1983). Reproductive competition in the communal acorn woodpecker: sisters destroy each other's eggs. *Nature*, **306,** 583–584.

Rohwer, S. & Spaw, C. D. (1988). Evolutionary lag versus bill-size constraints: a comparative study of the acceptance of cowbird eggs by old hosts. *Evolutionary Ecology*, **2,** 27–36.

Rothstein, S. I. (1975). An experimental and teleonomic investigation of avian brood parasitism. *Condor*, **77,** 250–271.

Skarphedinsson, K. H. (1982). Spörfuglar. *Fuglar* (Ed. by A. Gardarsson), Landvernd, Reykjavik.

Stouffer, P. C., Kennedy, E. D. & Power, H. W. (1987). Recognition and removal of intraspecific parasite eggs by starlings. *Animal Behaviour*, **35,** 1583–1584.

Vehrencamp, S. L. (1977). Relative fecundity and parental effort in communally nesting anis, *Crotophaga sulcirostris. Science*, **197,** 403–405.

Victoria, J. K. (1972). Clutch characteristics and egg discriminative ability of the African village weaverbird *Ploceus cucullatus. Ibis*, **114,** 367–376.

Wasenius, E. (1936). Om de i Finland funna typerna av gökägg och deras geografiska utbredning. (On the type of cuckoo eggs in Finland and their geographic distribution). *Ornis Fennica*, **8,** 147–153.

Witherby, H. F., Jourdain, F. C. R., Ticehurst, N. F. & Tucker, B. W. (1943). *The Handbook of British Birds.* Witherby, London.

Wyllie, I. (1981). *The Cuckoo.* Batsford, London.

Yom-Tov, Y. (1980). Intraspecific nest parasitism in birds. *Biological Reviews*, **55,** 93–108.

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