

Egg-morphs and host preference in the common cuckoo (*Cuculus canorus*): an analysis of cuckoo and host eggs from European museum collections

ARNE MOKSNES AND EIVIN RØSKAFT¹

Department of Zoology, University of Trondheim, N-7055 Dragvoll, Norway

(Accepted 21 June 1994)

(With 8 figures in the text)

An examination of about 12 000 clutches of European passerines that contained eggs of the common cuckoo (*Cuculus canorus*), held in museum egg-collections, revealed statistically significant correlations between the cuckoo and the host eggs within a clutch in volume, ground colour, and size and percentage coverage of the spots. Although most cuckoo eggs were yellowish, the range in coloration and the percentage coverage of spots indicate that in these respects the cuckoo eggs are distributed along a continuum. However, a similar distribution was also found among the pooled host eggs. These results provide some support for the 'host preference hypothesis', which states that each cuckoo female specializes on one particular host species.

By using a subjective classification, we found that there are at least 15 different cuckoo egg-morphs in Europe, but only 44% of the clutches contained cuckoo eggs of the egg-morph corresponding to the host eggs. The 'host preference hypothesis' therefore cannot provide a satisfactory explanation for the variation found among cuckoo eggs in Europe. However, 77% of the cuckoo eggs had been laid in nests of hosts with nesting sites similar to those of the main host of the egg-morph. This indicates that cuckoos also parasitize several species whose nest sites are similar to those of their main host. These results therefore provide support for the 'nest site hypothesis' which states that each cuckoo female parasitizes a group of host species with similar eggs or nest sites. The 'natal philopatry hypothesis' which states that female cuckoos may search for nests completely at random in their natal habitat is only weakly supported and can probably be rejected.

Most of the hosts, main and secondary, nest among low vegetation or on the ground, whereas tree-nesting species are seldom parasitized. The most frequently used hosts in the egg collections we examined were species of the *Acrocephalus* and *Sylvia* genera of warblers, all species that breed in low vegetation.

Contents

	Page
Introduction	626
Materials and methods	627
Sample size	627
Unsuitable and suitable hosts	631
Cuckoo egg-morphs	632
Volume	632
Ground colour	632
Size and cover of spots	632
Degree of mimicry	632
Nest site.	633
Statistical methods	634

¹Present address: Norwegian Institute for Nature Research, NINA, Tungasletta 2, 7005 Trondheim, Norway

Results	634
Parasitized hosts	634
Cuckoo egg-morphs	634
Volume	636
Ground colour	637
Size and cover of spots	637
Degree of mimicry	639
Distribution of ground colour and percentage coverage of spots	641
Nest site	641
Discussion	642
The use of egg collections for the study of cuckoo parasitism	642
Have hosts selected for the small size of cuckoo eggs?	642
Are there distinct cuckoo egg-morphs?	643
How are gentes maintained?	643
Nest site	645
Conclusion	646
References	647

Introduction

In the Old World, the common cuckoo (*Cuculus canorus*) is an obligate brood parasite that lays its eggs in the nests of a variety of different host species, mainly smaller passerines. The cuckoo lays a single egg, normally during the host's laying period, in the afternoon, when the host is frequently absent from the nest, so that the risk of the cuckoo being observed at the nest is low (Wyllie, 1981; Davies & Brooke, 1988). The parasite egg runs a higher risk of being rejected if the host observes the cuckoo laying in its nest (Davies & Brooke, 1988; Moksnes & Røskaft, 1989; Moksnes, Røskaft & Korsnes, 1993).

Because the cuckoo thereby dramatically reduces the host's breeding success, it has been obvious to naturalists that defences should have been evolved among the hosts to counteract such parasitism. Mechanisms of egg recognition by the host species have led to selection for host-egg mimicry by the cuckoo eggs (Baker, 1913, 1923, 1942; Brooke & Davies, 1988; Davies & Brooke, 1989; Higuchi, 1989; but see Harrison, 1968; M. G. Brooker & Brooker, 1989; L. C. Brooker, Brooker & Brooker, 1990, for alternative explanations). Common cuckoo eggs therefore often resemble those of the host, in both basic coloration and type of spotting, but are in most cases somewhat larger in size, although the eggs are still very small for a bird species of the size of an adult cuckoo (Lack, 1968). Descriptions of cuckoo eggs found in host nests have led to formulation of the 'specialist' or 'host preference' hypothesis (HPH; Brooke & Davies, 1991), which states that the common cuckoo, as a species, can be subdivided into several egg-colour morphs or gentes (singular: gens) (Jourdain, 1925; Chance, 1940; Baker, 1942; Lack, 1968; Wyllie, 1981; Brooke & Davies, 1991). Furthermore, this gentes theory states that each female cuckoo lays an egg of constant type, one that matches those of a single species (Chance, 1940; Baker, 1942; Lack, 1968). The most distinct of these gentes is probably the pale blue cuckoo egg, which is normally found in nests of the redstart (*Phoenicurus phoenicurus*) or in those of other hosts that lay pale blue eggs (cf. Tysse, 1993). So far no systematic analysis of these gentes has been made, and thus the actual number of cuckoo egg-morphs or gentes in Europe, or in other parts of the world, is not clear. However, Brooke & Davies (1988) quantified the differences, in ground colour and darkness, between the eggs of the cuckoo gentes present in Britain and found that these gentes differed significantly in both these characters. It is therefore well known that

several different cuckoo egg-morphs do occur in sympatry (Chance, 1940; Baker, 1942; Wyllie, 1981). None the less, only a few species are frequently used as hosts by the cuckoo in Europe (Baker, 1942; Glue & Morgan, 1972; Wyllie, 1981; Glue & Murray, 1984; Brooke & Davies, 1987; Moksnes & Røskft, 1987).

According to the HPH, each cuckoo-gens specializes on one particular host species, in whose nests it lays mimetic eggs. This hypothesis is supported by field observations of egg-laying cuckoo females made by Chance (1940) and Baker (1942)—despite some sources of error in their investigations—and even more convincingly by radio-tracking of egg-laying females (Wyllie, 1981; Dröscher, 1988). Host imprinting in the cuckoo is a necessary mechanism for maintaining host specialization according to the HPH. Brooke & Davies (1991), however, found no support for the existence of such imprinting.

An alternative hypothesis to the HPH is that each gens may parasitize a group of host species with similar eggs and nest sites, and searches for nests at random within this group (the 'nest-site hypothesis', NSH: Wyllie, 1981; Moksnes & Røskft, 1987). A third hypothesis is that cuckoos may search for nests completely at random in the habitat where they were born and reared. This latter possibility was put forward by Brooke & Davies (1991) as the 'Natal philopatry hypothesis' (NPH). There is some evidence from ringing recoveries that cuckoos do return to their natal habitat (Seel, 1977). The question as to whether the NPH could explain the existence of cuckoo egg mimicry has been discussed by Brooke & Davies (1991). If the cuckoos search for nests at random, host species that either occur at high densities, or have easily found nests, will stand the greatest chance of being parasitized. In uniform habitats, where one, or only a few, species predominate, random searching could result in most of the cuckoo's eggs being laid in the nests of one and the same host species, a necessary condition for the maintenance of egg mimicry. Examples of this situation may be seen in the excellent mimicry of the eggs of cuckoos that parasitize the meadow pipit (*Anthus pratensis*) which nests on the bogs and heaths of Northern Europe, and of those that parasitize great reed warblers (*Acrocephalus arundinaceus*) that nest in the Hungarian marshes (Southern, 1954). In fragmented habitats with a greater diversity of host species, on the other hand, one would expect that random searching would result in the cuckoos laying their eggs in the nests of many different species and that, in consequence, the eggs would show a poorer degree of mimicry (see also Harrison, C.J.O., 1968; Moksnes, Røskft & Korsnes, 1993).

In this paper we report on an examination of more than 12 000 cuckoo eggs held in museum egg-collections in Europe. We discuss the adaptations of cuckoos towards the host species in regard to egg size, ground colour, and the size and coverage of egg spots. We have also made a subjective classification of all the cuckoo eggs in an attempt to describe and discuss the different cuckoo egg-morphs in Europe and the cuckoo's adaptations with respect to egg variation. The results are finally considered in the light of the three hypotheses presented above.

Materials and methods

Sample size

We examined, during the years 1988–1993, the clutches of host eggs containing cuckoo eggs held in the collections of 27 different museums and private collections, in England, Sweden, Germany, Denmark, Switzerland, Finland, USA, The Netherlands, The Czech Republic, Hungary, Austria, Serbia (Vojvodina) and Norway. Altogether, 12 077 cuckoo eggs were examined, of which 11 870 were found in different host clutches (Table I). For each cuckoo egg, the location ($n = 11\,931$) and date (month, day) when collected

TABLE I

The number of cuckoo eggs found in nests of potential hosts in Europe, and the number of cuckoo eggs belonging to different morphs found in the nest of their corresponding host species. s/u = suitable/unsuitable hosts; nest sites: g = ground, l = low vegetation, t = trees, h = holes

Host	No. of cuckoo eggs	Nest site	s/u	Cuckoo eggs found in their corresponding host species	
				(n)	(%)
Reed warbler, <i>Acrocephalus scirpaceus</i>	2655	l	s	1258	47.4
Garden warbler, <i>Sylvia borin</i>	1266	l	s	1100	86.9
White/pied wagtail, <i>Motacilla alba</i>	832	g, l	s	451	54.2
Meadow pipit, <i>Anthus pratensis</i>	733	g	s	549	74.9
Red-backed shrike, <i>Lanius collurio</i>	708	l	s	69	9.7
Dunnock, <i>Prunella modularis</i>	547	l	s	2	0.4
Wren, <i>Troglodytes troglodytes</i>	516	h	s	0	0
Whitethroat, <i>Sylvia communis</i>	460	l	s	332	72.2
Robin, <i>Erithacus rubecula</i>	459	g	s	20	4.4
Great reed warbler, <i>Acrocephalus arundinaceus</i>	415	l	s	344	82.9
Sedge warbler, <i>Acrocephalus schoenobaenus</i>	315	l	s	114	36.2
Redstart, <i>Phoenicurus phoenicurus</i>	299	h	s	222	74.2
Tree pipit, <i>Anthus trivialis</i>	213	g	s	138	64.8
Yellow wagtail, <i>Motacilla flava</i>	197	g	s	126	64.0
Yellowhammer, <i>Emberiza citrinella</i>	195	g	s	8	4.1
Blackcap, <i>Sylvia atricapilla</i>	180	l	s	117	65.0
Marsh warbler, <i>Acrocephalus palustris</i>	141	l	s	27	19.1
Linnet, <i>Acanthis cannabina</i>	122	l	u	0	0
Greenfinch, <i>Chloris chloris</i>	110	l, t	u	9	8.2
Spotted flycatcher, <i>Muscicapa striata</i>	109	l, t	s	36	33.0
Lesser whitethroat, <i>Sylvia curruca</i>	94	l	s	62	66.0
Barred warbler, <i>Sylvia nisoria</i>	88	l	s	3	3.4
Willow warbler, <i>Phylloscopus trochilus</i>	82	g	s	0	0
Whinchat, <i>Saxicola rubetra</i>	82	g	s	22	26.8
Chiffchaff, <i>Phylloscopus collybita</i>	79	g	s	0	0
Wood warbler, <i>Phylloscopus sibilatrix</i>	76	g	s	0	0
Chaffinch, <i>Fringilla coelebs</i>	76	t	s	9	11.8
Reed bunting, <i>Emberiza schoeniclus</i>	72	g, l	s	3	4.2
Brambling, <i>Fringilla montifringilla</i>	53	t	s	41	77.4
Skylark, <i>Alauda arvensis</i>	50	g	s	21	42.0
Orphee warbler, <i>Sylvia hortensis</i>	45	l, t	s	40	88.9
Wheatear, <i>Oenanthe oenanthe</i>	39	g	u	14	35.9
Tawny pipit, <i>Anthus campestris</i>	32	g	s	6	18.8
Bullfinch, <i>Pyrrhula pyrrhula</i>	28	l, t	u	3	10.7
Corn bunting, <i>Emberiza calandra</i>	27	g, l	s	7	25.9
Stonechat, <i>Saxicola torquata</i>	27	g	s	0	0
Rock pipit, <i>Anthus spinoletta</i>	26	g	s	16	61.5
Grasshopper warbler, <i>Locustella naevia</i>	25	g, l	s	0	0
Nightingale, <i>Luscinia megarhynchos</i>	25	g	s	0	0
Woodlark, <i>Lullula arborea</i>	23	g	s	5	21.7
Grey wagtail, <i>Motacilla cinerea</i>	22	g	s	6	27.3
Pied flycatcher, <i>Ficedula hypoleuca</i>	21	h	u	16	76.2
Blackbird, <i>Turdus merula</i>	21	t	u	0	0
Woodchat shrike, <i>Lanius senator</i>	17	t	s	0	0
Cirl bunting, <i>Emberiza cirlus</i>	20	g, l	s	2	10.0
Redpoll, <i>Carduelis flammea</i>	15	l, t	u	0	0
Twite, <i>Carduelis flavirostris</i>	15	g	u	0	0
Aquatic warbler, <i>Acrocephalus paludicola</i>	14	l	s	8	57.1
Song thrush, <i>Turdus philomelos</i>	11	l, t	u	0	0

TABLE I (cont.)

Host	No. of cuckoo eggs	Nest site	s/u	Cuckoo eggs found in their corresponding host species	
				(n)	(%)
Sardinian warbler, <i>Sylvia melanocephala</i>	10	l	s	3	30.0
Bluethroat, <i>Luscinia svecica</i>	9	g	s	0	
Hawfinch, <i>Coccothraustes coccothraustes</i>	9	t	u	0	
Red-throated pipit, <i>Anthus cervinus</i>	8	g	s	4	
Icterine warbler, <i>Hippolais icterina</i>	8	t	s	0	
Dartford warbler, <i>Sylvia undata</i>	8	g, l	s	3	
Marmora's warbler, <i>Sylvia sarda</i>	8	l	s	3	
Lesser grey shrike, <i>Lanius minor</i>	8	l, t	s	0	
Crested lark, <i>Galerida cristata</i>	7	g	s	0	
Great tit, <i>Parus major</i>	7	h	u	0	
Black redstart, <i>Phoenicurus ochruros</i>	7	h	u	0	
House sparrow, <i>Passer domesticus</i>	7	h	u	2	
Great grey shrike., <i>Lanius excubitor</i>	6	l, t	u	0	
Lapland bunting, <i>Calcarius lapponicus</i>	6	g	s	3	
Rufous bush robin, <i>Cercotrichas galactotes</i>	5	l	s	0	
Goldfinch, <i>Carduelis carduelis</i>	5	t	u	0	
Ring ouzel, <i>Turdus torquatus</i>	4	g	u	4	
Tree creeper, <i>Certhia familiaris</i>	4	h	u	0	
Thrush nightingale, <i>Luscinia luscinia</i>	3	g	s	1	
Fieldfare, <i>Turdus pilaris</i>	3	t	u	0	
Tree sparrow, <i>Passer montanus</i>	3	h	u	2	
Ortolan bunting, <i>Emberiza hortulana</i>	3	g	s	0	
Wryneck, <i>Jynx torquilla</i>	2	h	u	1	
Shore lark, <i>Eremophila alpestris</i>	2	g	s	1	
Savi's warbler, <i>Locustella luscinioides</i>	2	g, l	s	0	
River warbler, <i>Locustella fluviatilis</i>	2	g	s	0	
Moustached warbler, <i>Acrocephalus melanopogon</i>	2	l	s	1	
Bonelli's warbler, <i>Phylloscopus bonelli</i>	2	g	s	0	
Cetti's warbler, <i>Cettia cetti</i>	2	g, l	s	1	
Olivaceous warbler, <i>Hippolais pallida</i>	2	l	s	0	
Olive-tree warbler, <i>Hippolais olivetorum</i>	2	l, t	s	0	
Booted warbler, <i>Hippolais caligata</i>	2	g	s	0	
Firecrest, <i>Regulus ignicapillus</i>	2	t	u	0	
Isabelline wheatear, <i>Oenanthe isabellina</i>	2	g	u	0	
Redwing, <i>Turdus iliacus</i>	2	g, l	u	0	
Magpie, <i>Pica pica</i>	2	t	u	0	
Short-toed tree creeper, <i>Certhia brachydactyla</i>	2	h	u	0	
Scarlet rosefinch, <i>Carpodacus erythrinus</i>	2	l	u	0	
Siskin, <i>Carduelis spinus</i>	2	t	u	0	
Black-headed bunting, <i>Emberiza melanocephala</i>	2	l	s	0	
Short-toed lark, <i>Calandrella cinerea</i>	1	g	s	0	
Bimaculated lark, <i>Melanocorypha bimaculata</i>	1	g	s	0	
White-winged lark, <i>Melanocorypha leucoptera</i>	1	g	s	0	
Starling, <i>Sturnus vulgaris</i>	1	h	u	1	
Azure-winged magpie, <i>Cyanopica cyana</i>	1	t	s	0	
Black-eared wheatear, <i>Oenanthe hispanica</i>	1	g	u	1	
Mistle thrush, <i>Turdus viscivorus</i>	1	t	u	0	
Rock thrush, <i>Monticola saxatilis</i>	1	g	u	1	
Spectacled warbler, <i>Sylvia conspicillata</i>	1	l	s	0	
Serin, <i>Serinus serinus</i>	1	l, t	u	0	
Canary, <i>Serinus canaria</i>	1	t	u	0	
Swallow, <i>Hirundo rustica</i>	1	h	u	0	

TABLE I (cont.)

Host	No. of cuckoo eggs	Nest site	s/u	Cuckoo eggs found in their corresponding host species	
				(n)	(%)
Marsh tit, <i>Parus palustris</i>	1	h	u	1	
Long-tailed tit, <i>Aegithalos caudatus</i>	1	h	u	0	
Bearded tit, <i>Panurus biarmicus</i>	1	l	u	0	
Nuthatch, <i>Sitta europaea</i>	1	h	u	1	
Rock bunting, <i>Emberiza cia</i>	1	g	u	0	
Rustic bunting, <i>Emberiza rustica</i>	1	g, l	s	0	
Snow bunting, <i>Plectrophenax nivalis</i>	1	g	u	0	
Calandra lark, <i>Melanocorypha calandra</i>	0	g	s		
Thekla lark, <i>Galerida theklae</i>	0	g	s		
Crag martin, <i>Ptyonoprogne rupestris</i>	0	(t)	s		
Reed-rumped swallow, <i>Hirundo daurica</i>	0	h	u		
House martin, <i>Delichon urbica</i>	0	h	u		
Sand martin, <i>Riparia riparia</i>	0	h	u		
Masked shrike, <i>Lanius nutricus</i>	0	t	s		
Golden oriole, <i>Oriolus oriolus</i>	0	t	u		
Rose-coloured starling, <i>Sturnus roseus</i>	0	h	u		
Spotted starling, <i>Sturnus unicolor</i>	0	h	u		
Waxwing, <i>Bombycilla garrulus</i>	0	t	u		
Siberian jay, <i>Perisoreus infaustus</i>	0	t	u		
Jay, <i>Garrulus glandarius</i>	0	t	u		
Nutcracker, <i>Nucifraga caryocatactes</i>	0	t	u		
Chough, <i>Pyrrhocorax pyrrhocorax</i>	0	h	u		
Alpine chough, <i>Pyrrhocorax graculus</i>	0	h	u		
Jackdaw, <i>Corvus monedula</i>	0	h	u		
Dipper, <i>Cinclus cinclus</i>	0	g, h	u		
Alpine accentor, <i>Prunella collaris</i>	0	g, h	u		
Fan-tailed warbler, <i>Cisticola juncidis</i>	0	g, l	s		
Blyth's reed warbler, <i>Acrocephalus dumetorum</i>	0	l	s		
Melodious warbler, <i>Hippolais polyglotta</i>	0	t	s		
Subalpine warbler, <i>Sylvia cantillans</i>	0	l	s		
Arctic warbler, <i>Phylloscopus borealis</i>	0	g	s		
Greenish warbler, <i>Phylloscopus trochiloides</i>	0	g	s		
Goldcrest, <i>Regulus regulus</i>	0	t	u		
Collared flycatcher, <i>Ficedula albicollis</i>	0	h	u		
Semi-collared flycatcher, <i>Ficedula semitorquata</i>	0	h	u		
Red-breasted flycatcher, <i>Ficedula parva</i>	0	h	u		
Black wheatear, <i>Oenanthe leucura</i>	0	g	u		
Blue rock-thrush, <i>Monticola solitarius</i>	0	g	u		
Willow tit, <i>Parus montanus</i>	0	h	u		
Sombre tit, <i>Parus lugubris</i>	0	h	u		
Siberian tit, <i>Parus cinctus</i>	0	h	u		
Crested tit, <i>Parus cristatus</i>	0	h	u		
Blue tit, <i>Parus caeruleus</i>	0	h	u		
Coal tit, <i>Parus ater</i>	0	h	u		
Penduline tit, <i>Remiz pendulinus</i>	0	h	u		
Corsican nuthatch, <i>Sitta whiteheadi</i>	0	h	u		
Rock nuthatch, <i>Sitta neumayer</i>	0	h	u		
Wallcreeper, <i>Tichodroma muraria</i>	0	h	u		
Spanish sparrow, <i>Passer hispaniolensis</i>	0	t	s		
Rock sparrow, <i>Petronia petronia</i>	0	h	u		
Snow finch, <i>Montifringilla nivalis</i>	0	h	u		
Citril finch, <i>Serinus citrinella</i>	0	t	u		

TABLE I (cont.)

Host	No. of cuckoo eggs	Nest site	s/u	Cuckoo eggs found in their corresponding host species	
				(n)	(%)
Arctic redpoll, <i>Carduelis hornemanni</i>	0	g, l	u		
Pine grosbeak, <i>Pinicola enucleator</i>	0	l, t	u		
Crossbill, <i>Loxia curvirostra</i>	0	t	u		
Parrot crossbill, <i>Loxia pytyopsittacus</i>	0	t	u		
Little bunting, <i>Emberiza pusilla</i>	0	g	s		
Cretzschmar's bunting, <i>Emberiza caesia</i>	0	g	s		
Yellow-breasted bunting, <i>Emberiza aureola</i>	0	l	s		
Total	11 870				

($n = 9759$) were noted. Notes on cuckoo and host clutch size and the cuckoo egg-morph ($n = 11\,905$) were also made. We also measured the length and breadth of a number of cuckoo ($n = 3730$) and host ($n = 2308$) eggs and we recorded the ground colour of cuckoo ($n = 1538$) and of host ($n = 1548$) eggs, using Kornerup & Wanscher's (1978) *Handbook of colour* (Fig. 1). In addition, we recorded the size and coverage of the spots on some cuckoo ($n = 1362$) and host ($n = 1327$) eggs. Finally, the degree of similarity between the cuckoo and host eggs ($n = 11\,540$) was recorded.

Unsuitable and suitable hosts

Many of the potential cuckoo hosts in Europe can be classified as being unsuitable as cuckoo hosts (see

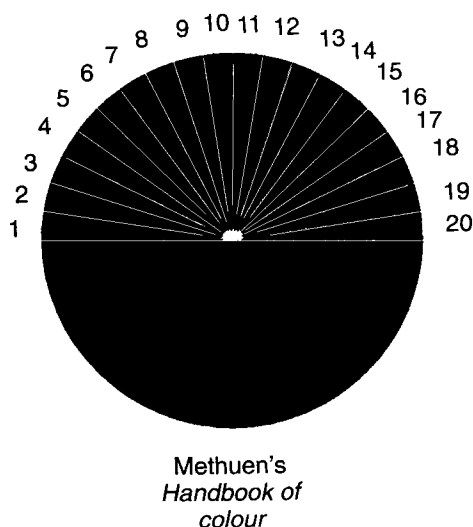


FIG. 1. The ground colours in Methuen's *Handbook of colour* (Kornerup & Wanscher, 1978) converted to a parametric scale, and used for the analyses in the present paper (yellow-red 1-4, yellow 5-8, green-yellow 9-12, green 13-16, blue-green 17-20).

Davies & Brooke, 1989; Moksnes *et al.*, 1990), either because they are hole-nesters or build their nests in concealed places, or because they feed their young with food unsuitable for the cuckoo chick, or because they have nests/eggs which are too big to permit successful ejection by the young cuckoo. It is therefore assumed that these species have not experienced any co-evolutionary arms race with the cuckoo. Some species, for example the greenfinch (*Chloris chloris*) may occupy an uncertain status in this respect (Moksnes *et al.*, 1990), but it is still regarded as being an unsuitable host (Table I). Those potential cuckoo hosts that are assumed to have experienced a co-evolutionary arms race with the cuckoo are classified as suitable hosts (Table I).

Cuckoo egg-morphs

The cuckoo egg-morphs were determined and named according to their resemblance to the host species or genus. (Note that we use the term egg-morph, and not gentes, in this study, because of our descriptions of cuckoo eggs.) This determination was made by comparing the colour and spottings of the cuckoo eggs with colour plates of the host species eggs as shown in the field guide of Harrison (1987). Both authors classified the egg-morphs independently. However, when there was disagreement in the classification, the whole clutch was photographed for later examination. In this later examination, the cuckoo egg was classified as belonging to the egg-morph it most resembled, but such eggs were given an uncertain egg-morph status. Some of these cuckoo eggs may therefore have occasionally been placed in the 'wrong' egg-morph category. Nevertheless, because our sample size is extremely large, these errors have probably had no influence on our major conclusions. In cases where the cuckoo egg-morph could be considered to resemble the eggs of several host species, the most common recorded host or genus was regarded as the main host of that particular cuckoo egg-morph.

Volume

The volumes of the cuckoo's and the host's eggs were estimated in accordance with the formula: $\text{Volume} = 0.51 * \text{Length} * \text{Breadth}^2 * 1000^{-1}$ (Hoyt, 1979).

Ground colour

When recording the ground colours of the cuckoo and host eggs, we used the Methuen *Handbook of colour* (Kornerup & Wanscher, 1978). It is possible to transform the ground colours tabulated in that handbook into a parametric system (Fig. 1). We chose the colour value of 2.5-Yellow-Red in the handbook as being 1. From 1 we followed the system as shown in Fig. 1, 20 being the colour value 10-Green.

Size and cover of spots

The size and degree of coverage of the spots on the cuckoo and host eggs were recorded. The coverages of spots on the cuckoo and host eggs were scored on a scale from 0 (0–10%) to 9 (90–99%) (Fig. 2). Similarly, the sizes of the spots were scored on a scale from small dots (1; about 0.1 mm) to large dots or stripes that were several millimetres in size (5; Fig. 2). The spots were scored both on the cap and on the central part of the eggs (Fig. 2). The method used in the present work was modified after those of Thomas, Thompson & Galbraith (1989) and Freeman (1988).

Degree of mimicry

The degree of mimicry of the host eggs by the cuckoo egg was classified according to a 5-degree scale. (1) Perfect mimicry: when the clutch was inspected, the cuckoo egg was hard to pick out except for normally

being larger than the host eggs. The colour and pattern of the cuckoo egg were similar to those of the host, and it was only possible to identify the cuckoo egg after a closer inspection of the clutch. (2) Good mimicry: the cuckoo egg was a good mimic of the host eggs, but small deviations in both colour and pattern (or in one of these 2 criteria) made the cuckoo egg relatively easy to distinguish after a closer inspection of the clutch. (3) Moderate mimicry: when the clutch was inspected it was easy to distinguish the cuckoo egg, but the colour or the pattern was in many respects similar to those of the host eggs. (4) Poor mimicry: the cuckoo egg was different from the host eggs, in both colour and pattern. (5) Non-mimetic: the cuckoo egg did not resemble the host eggs in any respect (see also Harrison, 1968).

Nest site

The nesting site of the host was classified in relation to sites in which the majority of the individuals within the species build their nests as: (1) birds breeding in trees, i.e. building their nests in trees or far above ground level; (2) birds breeding in low vegetation, i.e. birds breeding in bushes, in grass, on tree roots, on rocks, etc. close to the ground, normally 0–2 m above ground level; (3) birds breeding either in trees, or in low vegetation; (4) birds breeding on the ground; (5) birds breeding either on the ground or in the low vegetation; and (6) birds breeding in holes, i.e. birds breeding in holes or concealed places in trees, houses, under rocks, etc., places which the cuckoo normally is unable to reach. Details of breeding sites and of potential host species which, in the collections examined, had not been parasitized, were taken from Harrison (1987) and Cramp (1988, 1992).

In the present study, the largest species found to be parasitized in Europe was the magpie (*Pica pica*). All European passerines smaller than the magpie have therefore been included in our survey as being potential cuckoo hosts. In addition, we have also included the wryneck (*Jynx torquilla*) (i.e. a total of 160 potential host species).

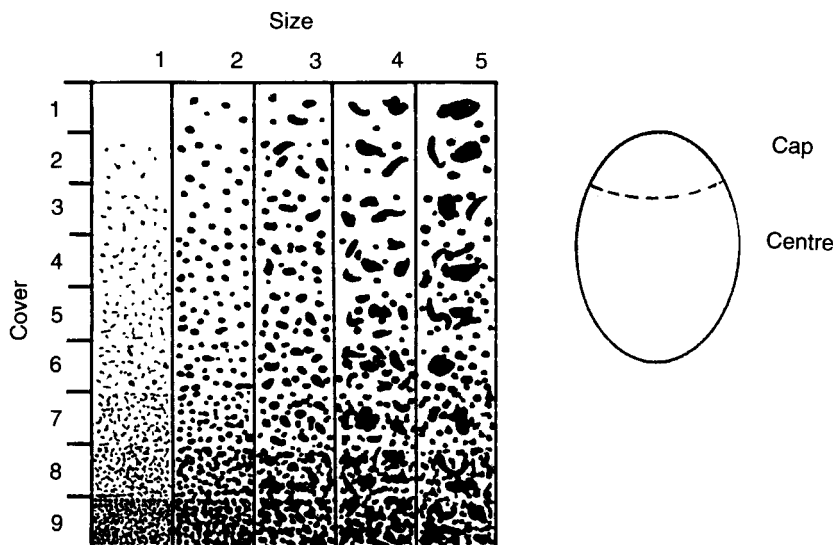


FIG. 2. The distribution of the degree of cover of the spots (vertical columns) and the size of the spots (horizontal columns), used in estimating these parameters on cuckoo and host eggs. The coverage and size of spots were recorded on both the cap and the central part of the eggs.

Statistical methods

The SPSSPC version 4.1 for Windows was used for analysing the data. For many of the statistical analyses, we used the mean values for the host species as a unit, but only in those cases in which the sample size of the species exceeded 10 cuckoo eggs and 10 host clutches, either for volume, ground colour, or coverage and size of spots. Except where otherwise stated, all tests are 2-tailed. In those cases in which the data were considered to show a normal distribution, we used parametric tests.

Results*Parasitized hosts*

Out of 160 potential host species in Europe, 108 (67.5%) in the collections examined were recorded as having been parasitized at least once. The most common hosts recorded were the reed warbler (*Acrocephalus scirpaceus*) ($n = 2655$), and the garden warbler (*Sylvia borin*) ($n = 1266$, Table I). Five species were parasitized between 501 and 1000 times, 23 between 50 and 500 times, 20 between 10 and 49 times, 58 species less than 10 times, while 52 species were not recorded as parasitized in this study (Table I).

When we compared the suitable and unsuitable hosts that had open, accessible nests (excluding the hole-nesters), we found a statistically significant higher number of parasitized clutches among the suitable than among the unsuitable hosts (Mann-Whitney-test: $U = 496$, $P < 0.001$).

Cuckoo egg-morphs

In the museum collections examined, at least 15 egg-morphs were recorded. These eggs were found in the nests of 108 different host species (Tables I, II). The cuckoo egg-morph most frequently recorded was the one termed *Sylvia* ($n = 3625$), which matches the eggs of the garden warbler, the lesser whitethroat (*S. curruca*), the blackcap (*S. atricapilla*) and some other *Sylvia* sp. warblers (and probably also the spotted flycatcher, *Muscicapa striata*). Furthermore, we found large numbers of a corresponding cuckoo egg-morph for the genus *Anthus* ($n = 1799$), which corresponds to some of the larks as well. The reed warbler ($n = 1708$) and the whitethroat (*Sylvia communis*) ($n = 1729$) also had corresponding cuckoo egg-morphs, as did some of the other species listed in Table II.

The blue egg-morph (Table II) corresponds to the egg coloration of many different host species, some of which breed in holes, others on the ground. However, since the main species (the redstart, Table I) is partly a hole-nester, yet the other hosts are ground-nesters, this egg-morph was placed in the hole-and-ground nesting category (but see also Tysse, 1993). The *Emberiza* egg-morph was the most difficult egg-morph to classify, although these cuckoo eggs mostly matched the host eggs of species belonging to that genus, in which egg patterning varies.

In addition to the 15 different egg-morphs listed in Table II, 38 cuckoo eggs were recorded as being similar in colour and spottings to the eggs of 16 other host species. At present, however, we can reach no conclusions as to whether these are different egg-morphs (although occurring very rarely) or simply occasional cuckoo egg-types. They have therefore been dealt with like the rest in the subsequent analyses.

Among the 31 most commonly parasitized species, the rate at which they were parasitized with their own corresponding cuckoo egg-morph varied between 0 and 89% (Table I). The species most commonly parasitized with their 'own' corresponding cuckoo egg-morph were the orphea

warbler (*Sylvia hortensis*) (88.9%), the garden warbler (86.9%), the great reed warbler (82.9%), the brambling (*Fringilla montifringilla*) (77.4%), the meadow pipit (74.9%), the redstart (74.2%) and the whitethroat (72.2%, Table I). The reason for the high value (76.2%) found for the pied flycatcher (*Ficedula hypoleuca*), which is an unsuitable host, is probably that this species is accidentally parasitized by blue-egg cuckoos in Finland (Tysse, 1993). The species which were rarely parasitized with their corresponding cuckoo egg-morph, but for which a corresponding cuckoo egg-morph was commonly recorded, were the greenfinch (8.2%), the red-backed shrike (*Lanius collurio*) (9.7%), the chaffinch (*Fringilla coelebs*) (11.8%), and the marsh warbler (*Acrocephalus palustris*) (19.1%). The latter had the same corresponding cuckoo egg-morph as the great reed warbler. However, most of the corresponding cuckoo egg-morphs of these species showed very limited distributions within the overall distributional ranges of the particular species.

The most commonly parasitized species for which no corresponding cuckoo egg-morph could be found was the wren (*Troglodytes troglodytes*) ($n = 516$). The dunnoek (*Prunella modularis*) ($n = 547$) has an egg corresponding to the blue cuckoo egg-morph of the redstart type. However, as shown in Table I, this type of cuckoo egg was found in only two dunnoek nests. A frequently parasitized species such as the robin (*Erithacus rubecula*) ($n = 459$) was not regularly parasitized with a corresponding cuckoo egg-morph (4.4%, Table I), although such an egg-morph was recorded 23 times, mostly in robin nests (Table II).

In the material as a whole, the cuckoo eggs belonging to the different morphs were found in the nests of their corresponding host species in 44.3% of all cases (Table II). For the different

TABLE II

The different cuckoo egg-morphs distinguished in the present study tabulated in relation to whether the cuckoo egg was found in the nests of the 'correct' species or in the nests of species with similar nest sites. Each cuckoo egg-morph was classified according to the egg colour and pattern of the host species it matched

Cuckoo egg-morph	Expected nest site of the cuckoo egg-morph	No. times recorded in the sample	No. times the morph was found in the 'correct' host species		No. times the morph was found in a similar nest site	
			(n)	(%)	(n)	(%)
<i>Fringilla</i>	Tree	98	50	51.0	51	52.0
Greenfinch	Tree + low	38	9	23.7	9	23.7
Yellow wagtail	Ground	297	126	42.4	204	68.7
<i>Sylvia</i>	Low veg.	3625	1315	36.3	2759	76.1
<i>Anthus</i>	Ground	1799	784	43.6	1069	59.4
White/pied wagtail	Ground + low	1093	457	41.8	748	68.4
Blue	Ground + hole	373	282	75.6	313	83.9
Robin	Low veg.	23	20	87.0	21	91.3
Reed warbler	Low veg.	1708	1258	73.7	1508	88.3
Sedge warbler	Low veg.	383	125	32.6	351	91.6
Whitethroat	Low veg.	1729	332	19.2	1505	87.0
Great reed warbler	Low veg.	416	371	89.2	403	96.9
<i>Lanius</i>	Low veg.	91	73	80.2	74	81.3
Orphean warbler	Low veg.	46	40	87.0	41	89.1
<i>Emberiza</i>	Ground	160	20	12.5	53	33.1
Others		26	6	23.1		
Total		11 905	5268	44.3	9109	76.5

morphs, this proportion varied between 12.5% (*Emberiza*) and 89.2% (great reed warbler). The blue, robin, reed warbler, *Lanius* and orphean warbler morphs also occurred at high frequencies in the nests of the appropriate host species.

The results of ANOVA-tests revealed that there were statistically significant differences between the different cuckoo egg-morphs in regard to all variables studied, i.e. in volume, ground colour, and size and coverage of spots (Table III).

Volume

The average volume of the cuckoo eggs in these collections that were measured was 3.133 cm^3 (S.D. = 0.361, $n = 3730$). Altogether, there was a positive (Pearson) correlation between the volume of the cuckoo egg and the volume of one randomly-chosen host egg in a clutch ($r = 0.176$, $n = 2234$, $P < 0.001$). Using the mean volume of the cuckoo's or the host's eggs as a unit, for those host species of which we recorded more than 10 cuckoo's and more than 10 host's egg volumes, yielding a sample comprising 50 different hosts, the correlation found between the cuckoo's and host's eggs (using the species as a unit) was still significantly positive ($r = 0.250$, $n = 50$, $P = 0.04$, one-tailed).

Furthermore, when we compared the mean egg volume of the cuckoo egg-morph (data from Table III) with the mean egg volume of its corresponding hosts (for those with samples of more than 10), we found a correlation which proved to be statistically significant ($r = 0.459$, $n = 15$, $P = 0.042$, one-tailed; Fig. 3). When the cuckoo egg volume was compared with latitude, using the mean cuckoo egg volume and the mean latitude in a country as units (and still using only samples above 10 for each latitude), there was no significant correlation ($r = 0.267$, $n = 17$, NS).

TABLE III

The average volume (cm^3), coloration (as explained in Fig. 1), and size and coverage of spots in the central part of the different cuckoo egg-morphs

Egg-morph	Volume			Colour			Size			Cover		
	Mean	S.D.	<i>n</i>	Mean	S.D.	<i>n</i>	Mean	S.D.	<i>n</i>	Mean	S.D.	<i>n</i>
<i>Fringilla</i>	3.00	0.37	90	10.1	3.7	68	3.9	1.2	73	2.5	1.6	73
Greenfinch	3.17	0.44	27	8.1	1.2	17	2.8	0.6	18	1.6	1.0	18
Yellow wagtail	3.12	0.38	130	7.0	1.3	86	3.4	1.1	73	6.4	2.1	73
<i>Sylvia</i>	3.10	0.35	971	7.6	1.4	414	3.9	0.8	295	3.3	1.6	295
<i>Anthus</i>	3.24	0.35	648	6.3	1.7	183	3.4	0.7	175	5.4	1.7	175
White/pied wagtail	3.15	0.31	392	7.7	0.9	149	2.9	0.6	137	4.9	1.7	138
Blue	3.16	0.32	240	15.5	2.1	107	1.1	0.6	118	1.1	0.5	118
Robin	3.27	0.44	20	6.6	1.4	14	3.3	0.7	18	2.8	0.8	18
Reed warbler	3.17	0.37	308	7.9	1.8	85	3.7	0.6	85	4.8	1.6	85
Sedge warbler	2.98	0.40	86	7.4	1.7	56	3.1	0.8	51	6.3	2.2	51
Whitethroat	3.02	0.39	326	7.4	1.4	200	3.4	0.8	138	4.8	1.9	138
Great reed warbler	3.04	0.35	293	10.4	2.3	61	3.3	0.7	80	1.9	1.2	80
<i>Lanius</i>	3.07	0.33	53	7.6	1.1	22	3.1	1.1	11	1.7	1.5	11
Orphean warbler	3.09	0.36	45	8.0	0.4	29	2.6	1.2	19	1.5	0.7	19
<i>Emberiza</i>	3.41	0.38	90	7.2	2.6	36	3.1	0.9	54	2.4	1.5	54
ANOVA-test	$P < 0.001$			$P < 0.001$			$P < 0.001$			$P < 0.001$		

Ground colour

We were able to compare the ground colours of the cuckoo and host eggs in 1356 clutches; ground colour was the same in 533 cases (39.3%). A Spearman rank-correlation analysis between the ground colour of the cuckoo's and host's eggs within the same clutch proved to be statistically significant ($r_{sp} = 0.359$, $n = 1356$, $P < 0.001$). Furthermore, when using the species as a unit, and averaging the colour values for those yielding sample sizes exceeding 10, the correlation (Pearson) between the ground colour of the cuckoo and host eggs was still statistically significant ($r = 0.632$, $n = 36$, $P < 0.001$).

The correlation between the average ground colour of the cuckoo egg-morphs (data from Table III) and their main hosts (for hosts for which the sample size exceeded 10, and considering each host as a single unit) was also statistically significant ($r = 0.970$, $n = 15$, $P < 0.001$; Fig. 4). This indicates that our subjective method in determining cuckoo egg-morphs is sufficient to sort out the different morphs on ground colour alone.

Size and cover of spots

Spearman rank-correlation analyses of host and cuckoo eggs in regard to size and coverage of spots all proved to be statistically significant (size cap, $r_{sp} = 0.284$, $n = 1257$; size centre, $r_{sp} = 0.318$, $n = 1255$; cover cap, $r_{sp} = 0.354$, $n = 1257$; cover centre, $r_{sp} = 0.354$, $n = 1255$; all $P < 0.001$). When the means, for those species for which there were data for more than 10 cuckoo and 10 host eggs, were compared by the same method as that used for volume and colour, the correlations obtained between the cuckoo and host eggs were still significant (size cap, $r_{sp} = 0.645$; size centre, $r_{sp} = 0.647$; cover cap, $r_{sp} = 0.592$; cover centre, $r_{sp} = 0.514$; all $n = 35$, all $P < 0.001$).

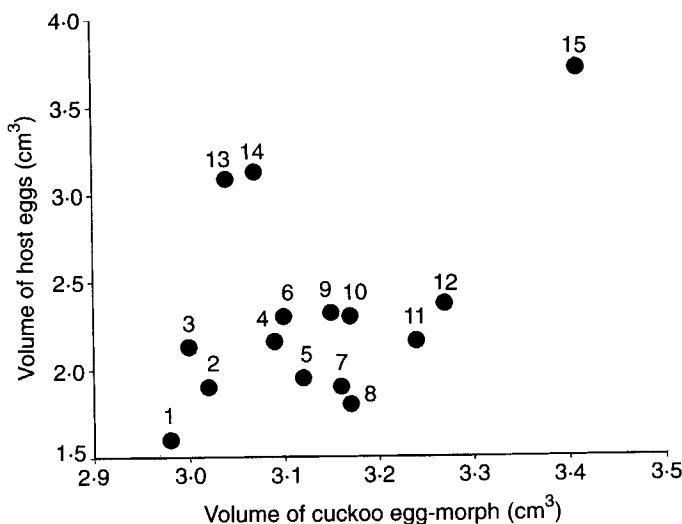


FIG. 3. The relationship between the average volume (cm³) of the different cuckoo egg-morphs and the average volume of the eggs of their main hosts ($r = 0.459$, $n = 15$, $P = 0.042$, one-tailed). Numbers indicate species: (1) sedge warbler, (2) whitethroat, (3) brambling, (4) orphean warbler, (5) yellow wagtail, (6) garden warbler, (7) redstart, (8) reed warbler, (9) white/pied wagtail, (10) greenfinch, (11) meadow pipit, (12) robin, (13) great reed warbler, (14) red-backed shrike, (15) corn bunting.

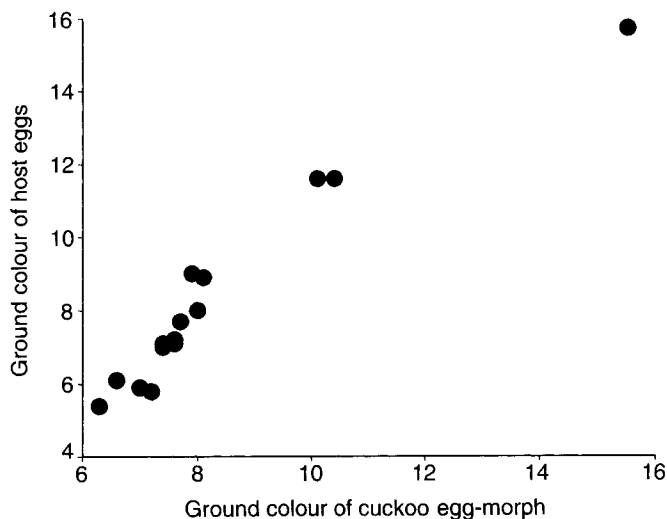


FIG. 4. The relationship between the average ground colour (see Fig. 1) of the different cuckoo egg-morphs and the average ground colour of the eggs of their main hosts ($r = 0.970$, $n = 15$, $P < 0.001$).

In addition, the Spearman rank-correlations between the coverage of the spots on the cuckoo egg-morphs (data from Table III) and on the eggs of their main hosts (for hosts for which sample size exceeded 10 and considering each host as a separate unit) were statistically significant (cover cap, $r_{sp} = 0.888$; cover centre, $r_{sp} = 0.915$; Fig. 5; $n = 15$, $P < 0.001$ for both). Furthermore, the Spearman rank-correlations between the size of the spots on the cuckoo egg-morphs and on the

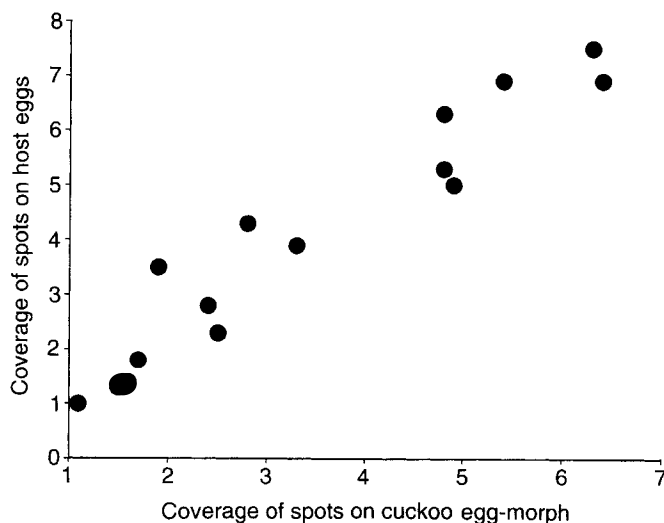


FIG. 5. The relationship between the average percentage of cover of spots (see Fig. 2) on the central part of the different cuckoo egg-morphs and on the eggs of their main hosts ($r = 0.915$, $n = 15$, $P < 0.001$).

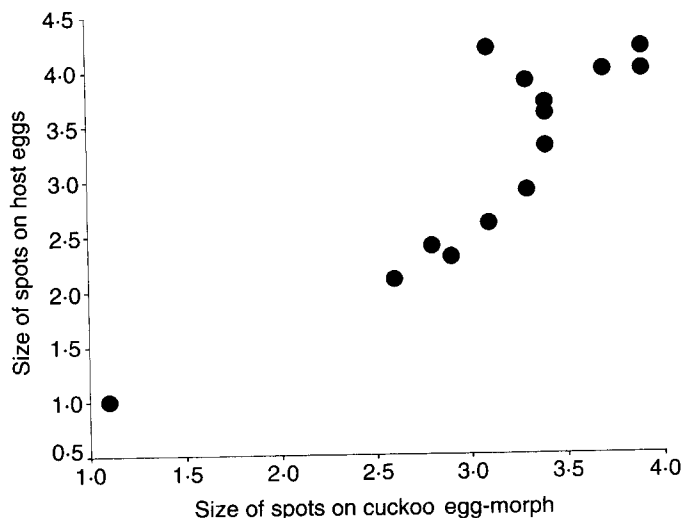


FIG. 6. The relationship between the average size of the spots on the central part (see Fig. 2) of the different cuckoo egg-morphs and on the eggs of their main hosts ($r = 0.817$, $n = 15$, $P < 0.001$).

eggs of their main hosts were also statistically significant (size cap, $r_{sp} = 0.833$; size centre, $r_{sp} = 0.817$; Fig. 6; $n = 15$, $P < 0.001$, for both). This indicates that our subjective method in determining potential cuckoo egg-morphs on the basis of ground colour and size and cover of spots is sufficient when the method is based on these three characters combined.

Degree of mimicry

Of the 11 540 cuckoo eggs that were compared with the host's eggs, 587 (5.1%) were classified as perfect mimics (1), 2851 (24.7%) as good mimics (2), 4291 (37.2%) as moderate mimics (3), 2414 (20.9%) as poor mimics (4), and 1397 (12.1%) as non-mimetic (5) (Fig. 7).

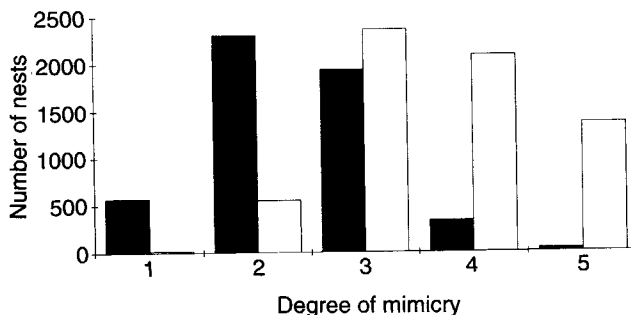


FIG. 7. Proportion of cuckoo eggs laid in different categories of nests in relation to the degree of mimicry between the cuckoo egg and the host eggs (1: perfect mimicry; 2: good mimicry; 3: moderate mimicry; 4: poor mimicry; 5: no mimicry; see text for further explanations). Solid bars indicate the proportion found in the nests of host species that 'belong' to the particular egg-morph and open bars the proportion found in the nests of species that do not. $n = 11\ 540$.

A correspondence was found between the cuckoo's egg and the host eggs, in that the cuckoo's egg had been laid in the nests of those host species that were assigned to the same egg-morph in 44.8% ($n = 5169$) of all instances for which the degree of mimicry had been scored (Fig. 7). In these nests, the median degree of mimicry was 2. However, for the cuckoo eggs found in the nests of species other than those parasitized by the particular egg-morph ($n = 6371$, 55.2%), the median degree of mimicry was 4 ($\chi^2 = 4091$, $d.f. = 4$, $P < 0.001$, Fig. 7).

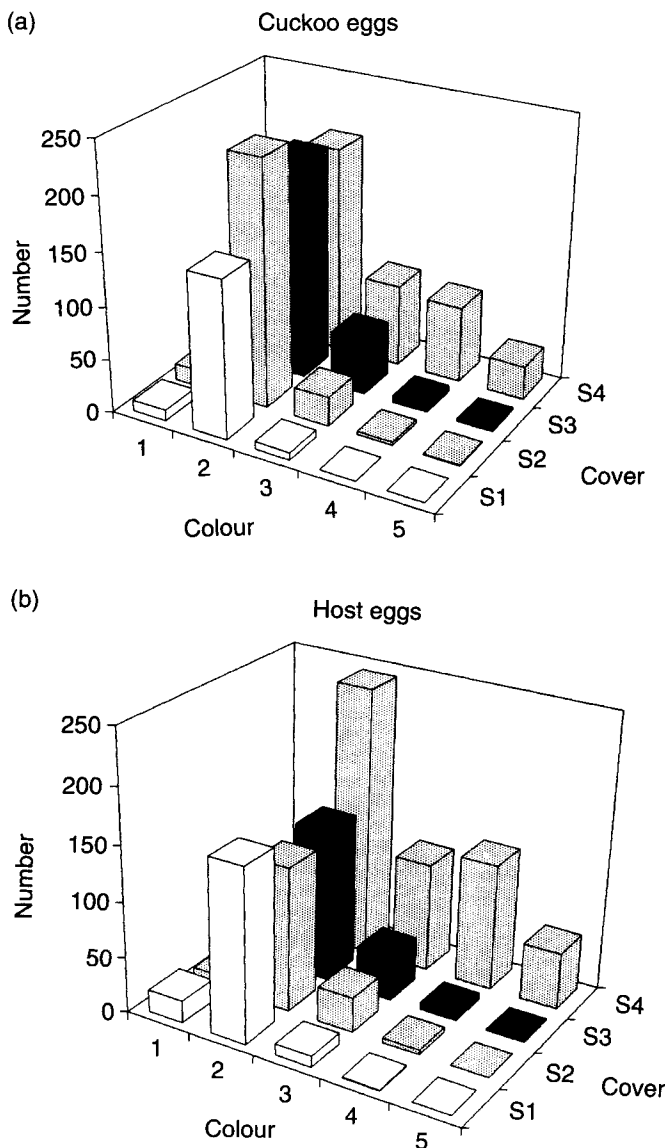


FIG. 8. The distribution of the ground coloration and of the coverage of spots found (a) on the central parts of cuckoo eggs ($n = 1113$) and (b) on host eggs ($n = 1097$). Colour: 1 = yellow-red, 2 = yellow, 3 = green-yellow, 4 = green, 5 = blue-green. Coverage degrees: S1 = 0–19%, S2 = 20–39%, S3 = 40–59%, S4 = 60–100%.

Distribution of ground colour and percentage coverage of spots

Figure 8a indicates the distribution among the cuckoo eggs of two variables, ground colour and cover of the spots on the central part of the egg. They clearly show a continuous distribution, although most of the cuckoo eggs show a clustering in the yellowish parts of the spectrum. However, the distribution of the same two variables among the pooled host eggs was similar to that for the cuckoo eggs (Fig. 8b).

Nest site

As pointed out earlier, the cuckoo eggs belonging to the different morphs were found in the nests of their 'correct' species in 44.3% of all cases (Table II). However, when we also included those host species that built their nests in sites similar to those of the main host, then 76.5% ($n = 9109$) of the cuckoo eggs were found either in nests of the 'correct' species, or in those of species nesting in similar habitats (Wilcoxon matched pairs test, $Z = 2.12$, $n = 15$, $P = 0.034$, Table II; a variation between 23.7% and 96.9%, median = 81.3%, for the different cuckoo egg-morphs). The most common nest-sites of such hosts were in the 'low vegetation' habitat, and these egg-morphs were found in nests of either the main host or in nests of hosts nesting in habitats similar to those of their main host at a median rate of 88.7% (Table II). However, ground-nesting species may very well be under-represented in egg collections, owing to the difficulties that collectors experience in finding the nests of species that breed on the ground. Nonetheless, a high frequency of parasitism in types of nesting sites similar to those of the main host was also found for the ground-nesting species, with the exception of only one egg-morph (median 59.4%, Table II). Eight (or at most 10) of the 15 egg-morphs were correlated with host species that breed in low vegetation, while only one was correlated with tree-breeding birds (Table II). Interestingly enough, we recorded a cuckoo egg-morph for only 12% of all tree-nesting passerines, a frequency similar to that recorded for hole-nesting birds (8%), while the corresponding value for those breeding in low vegetation was 48% (Table IV). Also, a greater number of cuckoo egg-morphs were found for ground-nesting birds (40%) than for tree-nesting species.

TABLE IV

Number of species parasitized by the common cuckoo, number of species in Europe that potentially could be parasitized by the common cuckoo, and the percentage of hosts in Europe with a corresponding cuckoo egg-morph. The data are tabulated in relation to the nesting sites of the hosts

Nest site	No. of species parasitized (present study) (No. of nests in brackets)	No. of species in Europe that potentially could be parasitized	Percentage of parasitized hosts with cuckoo egg-morph
Holes	15 (873)	40	8
Trees	14 (201)	27	12
Low vegetation—trees	10 (335)	11	36
Low vegetation	22 (7038)	25	48
On ground—low vegetation	10 (991)	12	42
On ground	37 (2432)	45	40
Total	108 (11870)	160	

Discussion

The use of egg collections for the study of cuckoo parasitism

The immense size of the egg collection, comprising more than 12 000 clutches, which we have studied, makes a unique and valuable source of information about egg-morphs and host usage among cuckoos. It is important, however, to bear in mind that such museum collections may be biased sources of data, for several reasons. There are at least four possible types of bias or error which can be pinpointed.

1. Nests that contain cuckoo eggs which show a low degree of mimicry with the host's eggs will be more conspicuous and will therefore most probably be collected at a higher rate. On the other hand, this bias will be counteracted by the fact that many host species reject non-mimetic cuckoo eggs, and that the rejection rate increases as the degree of mimicry decreases (Davies & Brooke, 1988, 1989; Brown *et al.*, 1990; Braa, Moksnes & Røskaft, 1992; Moksnes, 1992). The proportion of nests actually parasitized with cuckoo eggs with a poor degree of mimicry may therefore be underestimated in museum collections, because many of these eggs would already have been ejected by the hosts. In particular, unusual hosts may be under-represented in museum collections because many of them reject cuckoo eggs at a higher rate than the regular hosts do (Davies & Brooke, 1989; Moksnes *et al.*, 1990).

2. The searching patterns of different collectors may lead to an over-representation of some species in the collections. Some collectors are known to have specialized on one or a few species and collected large numbers of clutches from certain areas. This has obviously been the case in the present study, for example for the reed warbler in Denmark, the garden warbler in the vicinity of Berlin, the red-backed shrike in the vicinity of Leipzig, in Germany, and the redstart in Finland (see also Wasenius, 1936).

3. Clutches from easily found nests may be over-represented compared to those from nests which are difficult to find. For example, nests in trees would normally be easier to find, but harder to reach, than nests well hidden in low vegetation or on the ground. In the present study, cuckoo eggs were rarely found to have been collected from tree-nesting species. However, such bias would not seem to underlie the tree- to ground-nesting relationship with the number of egg-morphs which we found.

4. There is also a possibility that some of the clutches found in museum collections have been faked, i.e. had cuckoo eggs added later for exhibition purposes (Baker, 1942), or that some of the clutches contain odd eggs, laid by the same host female, which have been mistaken for a cuckoo's egg.

When analysing museum collections, it is impossible to check for such sources of error. However, the large sample-size (>12 000 cuckoo eggs) should in all probability obviate any systematic tendencies towards bias due to different collectors, because we would expect different collectors to be biased in different ways. Similarly, the large sample size should minimize other possible errors such as parasitism by other passerines, or 'faked' clutches.

Have hosts selected for the small size of cuckoo eggs?

The cuckoo lays smaller eggs in relation to its body size than any other bird of similar size (2.4% of its body weight; Lack, 1968). In this study, we have found a statistically significant, positive correlation between the size of the host's and the cuckoo's eggs. Since, in reports of earlier experiments (Moksnes & Røskaft, 1988, 1992; Braa *et al.*, 1992), we have presented evidence that some potential host species (chaffinch, brambling, reed bunting (*Emberiza*

schoeniclus) and willow warbler (*Phylloscopus trochilus*)) have the ability to discriminate against the cuckoo's eggs, on the basis of the size difference, this correlation supports the view that host behaviour is the selective agent responsible for the evolution of small eggs in the cuckoo. The willow warbler also rejects eggs that are highly mimetic in colour yet considerably smaller in size than cuckoo's eggs, namely those of the great tit (*Parus major*) (Moksnes & Røskaft, 1992). The fact that this species, in spite of showing strong rejection behaviour and behaving very aggressively towards cuckoos (Moksnes *et al.*, 1990), is unimportant as a cuckoo host (Table I), suggests that the cuckoo gens that once parasitized willow warblers has become extinct, because of the hosts' ability to reject the greater-sized cuckoo eggs. An evolution of even smaller eggs in the cuckoo, necessary for successful competition with the willow warbler in their co-evolutionary arms race, was probably restricted by other constraints. These results support the view of Baker (1942) and Davies & Brooke (1988), but contradict the view of L.C. Brooker & Brooker (1990), who have suggested that the evolution of cuckoo egg size (like that of colour mimicry and crypsis) may be explained as the direct result of interspecific and intraspecific egg replacement by competing female cuckoos. According to their hypothesis, rejection by the host is therefore an unconvincing explanation for the small size of cuckoo's eggs.

Are there distinct cuckoo egg-morphs?

In this study we found statistically significant positive correlations between the cuckoo's and host's eggs in relation to size (volume), ground colour, and size and coverage of spots. As the basis for these analyses, we used the data for (1) all parasitized clutches, (2) the mean value for each host species and the cuckoo eggs with which it was parasitized and (3) the mean value for each cuckoo egg-morph and the corresponding host species. In all these three cases, the correlations were statistically significant, although they only provided a partial explanation for the overall variation shown by the cuckoo eggs for any of these variables. These results therefore indicate that strongly developed adaptations exist between the cuckoo and its hosts and thus provide some support for the gentes theory. However, they do not indicate how distinct the gentes are, nor do they exclude other explanations. This is because the distribution of the variables, egg colour and coverage and size of the spots of cuckoo eggs, exhibits a continuous pattern that is similar to that of the eggs of all the potential host species.

The method used to classify the cuckoo egg-morphs in this study can be disputed. Obviously, we have not classified any gentes, because a cuckoo gens evolves in response to the rejection behaviour of the host. Some of these gentes could therefore lay eggs that resemble the eggs of types of hosts other than those they were intended to mimic. Classifying cuckoo egg-morphs by using good quality illustrations of eggs would, therefore, seem to be an appropriate method. Even by using this subjective method, we were able to classify at least 15 different cuckoo egg-morphs. These results are supported by the fact that the results of the ANOVA-tests show that the volume, colour and patterns of size and coverage of spots on the cuckoo eggs were all significantly different from an equal distribution, thus indicating the existence of several different cuckoo egg-morphs.

How are gentes maintained?

We here consider three of the hypotheses which have been proposed to explain the evolution of the host mimicry of cuckoo eggs.

The 'host preference hypothesis' (HPH)

According to this hypothesis we would predict that most cuckoo eggs should closely match those of the host. Furthermore, each different cuckoo egg-morph should be found in nests which contain the host eggs to which it corresponds. Our results only slightly support these two predictions. In only 5.1% of all cases was the cuckoo's egg regarded as a perfect mimic of the host's eggs, although 24.7% showed good mimicry. Also, the cuckoo egg-morph, as defined by our subjective method, was found in the nest of its corresponding host species in only 44.3% of the cases. Therefore, the HPH cannot provide a satisfactory explanation of the variation found among cuckoo eggs in Europe.

The 'nest site hypothesis' (NSH)

According to this hypothesis we would predict that each cuckoo gens parasitizes a group of host species with similar eggs and nest sites. As many as 76.5% of all the cuckoo eggs were laid in nests of either the 'correct' species, or of species with nesting sites similar to those of the main host. These results therefore do yield some support for the NSH. This hypothesis is further supported by some field observations from Norway, which show that cuckoos of the meadow pipit gens also parasitize reed buntings and Lapland buntings (*Calcarius lapponicus*), both species whose nest site and egg appearance are quite similar to those of the main host (Moksnes & Røskaft, 1987), at a frequency approximately proportional to their abundance in the area studied. The fact that no parasitism was observed of either the fieldfare (*Turdus pilaris*) or the brambling, both of which are very numerous birds in the same area (with obvious chances of interacting with cuckoos) but which nest in trees, also indicates that the cuckoo does not search for nests at random, but prefer hosts with certain kinds of nest site (Moksnes & Røskaft, 1987).

In Central Europe the most frequently recorded cuckoo egg-morph, the one we termed *Sylvia*, mimics the eggs of the garden warbler, lesser whitethroat, blackcap and those of a few other species (but see also Moksnes *et al.*, 1993). Since the nesting sites of all these species are in low vegetation, this could also illustrate a situation where the cuckoo parasitizes a group of species with comparable eggs and nest sites. A similar situation may exist for other species: for instance, the great reed warbler cuckoo has eggs that also mimic the eggs of the marsh warbler (see also Wyllie, 1981). Furthermore, the egg-morph that mimics the eggs of the pipits (*Anthus*) also mimics well the eggs of some of the larks, of some sparrows and of other ground-nesting birds. Similarities between the main host and other birds breeding in similar habitats have also been found for other cuckoo egg-morphs. The NSH seems therefore to provide a better explanation than the HPH for the variation found in cuckoo eggs in Europe.

The 'natal philopatry hypotheses' (NPH)

According to the NPH, better mimicry is to be expected in uniform than in fragmented habitats (see Brooke & Davies, 1991). Even though there are few data about the actual habitats for the localities where the parasitized clutches were collected, four host species are assumed to represent a more uniform habit than the others. These four are among the most common hosts, as shown in Table I, and are: the meadow pipit (most of the clutches from the bogs and heaths of northern Europe), the great reed warbler (from the marshes of Hungary and adjacent areas), the

brambling (from the subalpine birch forests of Fennoscandia) and the redstart (from the taiga of Finland and adjacent areas). Between 74.2% and 82.9% of the eggs of the cuckoo gentes mimicking these species were found in the nests of the corresponding host species. However, meadow pipits in England, great reed warblers in Hungary, bramblings and redstarts in Finland were parasitized with 86.8% ($n = 314$), 95.5% ($n = 506$), 84.8% ($n = 46$) and 100% ($n = 143$) of their corresponding cuckoo egg-morphs, respectively. These frequencies, all related to uniform habitats, are much higher than those found for the remaining samples, a fact that supports the NPH.

On the other hand, if the cuckoo searches for nests at random, one would expect that the different hosts would be parasitized in proportion to the abundance and accessibility of their nests. However, this was not the case: significantly fewer clutches of unsuitable hosts (and among them many very abundant species with easily accessible nests) than of suitable hosts were parasitized. As discussed above, rejection behaviour by the hosts will have an influence on the frequencies of parasitism derived from museum collections. Since experimental evidence shows that unsuitable hosts have a significantly lower rejection rate than most suitable hosts (Davies & Brooke, 1989; Moksnes *et al.*, 1990), this is obviously not a source of error in the present comparison. Our results therefore indicate that the cuckoo does not search for nests at random, but practises some sort of host preference. These results are in accordance with those of Glue & Murray (1984), who presented the parasitism rates for 28 British hosts, including five unsuitable ones, for the period 1939–82, based on the nest record cards of the British Trust for Ornithology. This material also showed that parasitism rates for suitable hosts were higher than those for unsuitable hosts. This counter-argument to the NPH has also been discussed by Brooke & Davies (1991). Our results therefore only partially support the NPH.

Nest site

One can only speculate at present as to why so few tree-nesting species are used by the cuckoo as hosts. A simple explanation is that many of these are unsuitable hosts, such as the thrushes and several seed-eating finches. Another reason may be that tree-nesting species have evolved strong rejection behaviour (e.g. chaffinch, brambling and the icterine warbler (*Hippolais icterina*) (Moksnes *et al.*, 1990) because of having formerly been heavily parasitized. There are even indications that one cuckoo egg-morph (*Fringilla*), associated with a tree-nesting species, seems to be experiencing some difficulty in surviving, because of the well-developed egg recognition mechanisms possessed by its usual hosts, the brambling and the chaffinch (Moksnes & Røskoft, 1987; Braa *et al.*, 1992; Moksnes, 1992).

An alternative explanation may be that selective pressure from the cuckoo has forced many European passerines to breed in dense, low-growing vegetation or on the ground, where the nest can be more easily concealed from the cuckoo. The cuckoo normally searches for nests from perches, keeping a watch for potential hosts building their nests below (Davies & Brooke, 1988; Alvarez, 1993). This idea implies that there should be relatively fewer tree nesters and more low-vegetation nesters in Europe than in areas where parasitism by cuckoos does not exist. On the other hand, hosts may also have evolved the habit of breeding in more concealed places near the ground as a defence against predators. However, cuckoo parasitism may exert a greater selection pressure on the host than nest predation because most passerines will re-nest after suffering predation, whereas successful cuckoo parasitism frequently results in a complete failure of reproduction for the entire season (Lack, 1968; Rothstein, 1990). Nevertheless, since the

predation pressure on host nests in any case seems to be lower near the ground than in trees (Moksnes & Røskaft, 1987), potential predator avoidance may also be of importance for the cuckoo in its search for suitable nests. In Japan, however, the cuckoo has recently started to parasitize a tree-nesting species, the azure-winged magpie (*Cyanopica cyana*) at a high rate (Yamagishi & Fujioka, 1986; Nakamura, 1990).

Conclusion

We conclude that the relatively low degree of 'host specialization' of the cuckoo (44.3%) found in the present study, may reflect the true situation, indicating that the cuckoo is a more generalistic species than it is usually thought to be. These data also fit with the lack of evidence for host imprinting found by Brooke & Davies (1991). However, some kind of host preference is obviously shown by different female cuckoos, a fact which is supported by the significant correlations found for all the recorded variables between cuckoo's and host's eggs. Although relatively small proportions of the host nests were parasitized by a corresponding cuckoo egg-morph, our results also clearly indicate that the cuckoo frequently parasitizes other host species that have nest sites similar to those of their main host. These results are clearly in favour of the nest site preference hypothesis and discriminate against the natal philopatry hypothesis. The female cuckoo probably searches for nests in similar habitats to those frequented by its main host, and perhaps uses the nests of other species when she is unable to find host nests of her own egg-morph by the time she is ready to lay. The cuckoo is thus not a perfect specialist, rather a semi-generalist.

Although it is possible to distinguish different cuckoo egg-morphs that resemble the eggs of particular host species, the results of the present study also indicate that there are no clear-cut differences between the egg-morphs. Many of the cuckoo eggs are perfect mimics of some of the host eggs, but there are also some variants, which do not resemble any of the eggs of the present hosts. However, the variability of the cuckoo's eggs ensures that some strains may survive into the future as long as some few host species exist which will accept small proportions of cuckoo eggs.

We are indebted to the staff of the British Museum (Natural History), Tring; Zoological Museum, Oslo; University of Trondheim, the Museum; Zoological Museum, Bergen; Stavanger Museum, Museum of Natural History, Gothenburg; Zoological Museum, Lund; Museum of Natural History, Copenhagen; Naturhistoriska Centralmuseet, Helsinki; Svenska Riksmuseet, Stockholm; Museum für Naturkunde der Humboldt-Universität zu Berlin; Museum d'Histoire naturelle, Genève; Zoologisches Forschungsinstitut und Museum Alexander König, Bonn; Burke Museum, University of Washington, Seattle; Western Foundation of Vertebrate Zoology, Los Angeles; Naturhistorisches Museum, Bern; Naturkundemuseum, Leipzig; Rijksmuseum van Natuurlijke Historie, Leiden; Staatliches Museum für Naturkunde in Stuttgart; National Museum Natural History, Praha; Natur-Museum Senckenberg, Frankfurt am Main; Hungarian Natural History Museum, Budapest; Naturhistorisches Museum, Wien; Moravské ornitologické sdružení, Prerov. We are also indebted to J. Rasajski and V. Gavrilov, Vrsac, Vojvodina and M. Haller, Rothrist, Switzerland, for allowing us to examine their private collections of cuckoo eggs, to A. T. Braa for making some of the cuckoo egg examinations, to M. de L. Brooke, H. L. Gibbs, L. Kiff, R. B. Payne, S. Rohwer, S. I. Rothstein, S. Sealy and B. E. Sæther for valuable comments on an earlier draft of the manuscript, and to P. A. Tallantire for improving the English. This study was supported by grants from the Nordic Society for Wildlife Research, the Nansen Foundation and the Norwegian Society for Science and the Humanities.

REFERENCES

- Alvarez, F. (1993). Proximity of trees facilitates parasitism by cuckoos *Cuculus canorus* on rufous warblers *Cercotrichas galactotes*. *Ibis* **135**: 331.
- Baker, E. C. S. (1913). The evolution of adaptation in parasitic cuckoo's eggs. *Ibis* **1913**: 384–398.
- Baker, E. C. S. (1923). Cuckoos' eggs and evolution. *Proc. zool. Soc. Lond.* **1923**: 277–294.
- Baker, E. C. S. (1942). *Cuckoo problems*. London: Witherby.
- Braa, A. T., Moksnes, A. & Røskaft, E. (1992). Adaptations of bramblings and chaffinches towards parasitism by the common cuckoo. *Anim. Behav.* **43**: 67–78.
- Brooke, M. de L. & Davies, N. B. (1987). Recent changes in host usage by cuckoos *Cuculus canorus* in Britain. *J. Anim. Ecol.* **56**: 873–883.
- Brooke, M. de L. & Davies, N. B. (1988). Egg mimicry by cuckoos *Cuculus canorus* in relation to discrimination by hosts. *Nature, Lond.* **335**: 630–632.
- Brooke, M. de L. & Davies, N. B. (1991). A failure to demonstrate host imprinting in the cuckoo (*Cuculus canorus*) and alternative hypotheses for the maintenance of egg mimicry. *Ethology* **89**: 154–166.
- Brooker, L. C. & Brooker, M. G. (1990). Why are cuckoos host specific? *Oikos* **57**: 301–309.
- Brooker, L. C., Brooker, M. G. & Brooker, A. M. H. (1990). An alternative population/genetics model for the evolution of egg mimesis and egg crypsis in cuckoos. *J. theor. Biol.* **146**: 123–143.
- Brooker, M. G. & Brooker, L. C. (1989). 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.
- Brown, R. J., Brown, M. N., Brooke, M. de L. & Davies, N. B. (1990). Reactions of parasitized and unparasitized populations of *Acrocephalus* warblers to model cuckoo eggs. *Ibis* **132**: 109–111.
- Chance, E. P. (1940). *The truth about the cuckoo*. London: Country Life.
- Cramp, S. (Ed.). (1988). *Handbook of the birds of Europe, the Middle East and North Africa. The birds of the Western Palaearctic 5: Tyrant flycatchers to thrushes*. Oxford: Oxford University Press.
- Cramp, S. & Brookes, D. J. (Eds). (1992). *Handbook of the birds of Europe, the Middle East and North Africa. The birds of the Western Palaearctic 6: Warblers*. Oxford: Oxford University Press.
- Davies, N. B. & Brooke, M. de L. (1988). Cuckoos versus reed warblers: adaptations and counteradaptations. *Anim. Behav.* **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. I. Host egg discrimination. *J. Anim. Ecol.* **58**: 207–224.
- Dröscher, L. (1988). A study on radio-tracking of the European cuckoo (*Cuculus canorus canorus*). *Proc. Int. 100 Do-G meeting*: 187–193.
- Freeman, S. (1988). Egg variability and conspecific nest parasitism in the *Ploceus* weaverbirds. *Ostrich* **59**: 49–53.
- Glue, D. & Morgan, R. (1972). Cuckoo hosts in British habitats. *Bird Study* **19**: 187–192.
- Glue, D. & Murray, R. (1984). Cuckoo hosts in Britain. *BTO News* No. 134: 5.
- Harrison, C. J. O. (1968). Egg mimicry in British cuckoos. *Bird Study* **15**: 22–28.
- Harrison, C. (1987). *A field guide to the nests, eggs and nestlings of European birds*. London: Collins.
- Higuchi, H. (1989). Responses of the bush warbler *Cettia diphone* to artificial eggs of *Cuculus* cuckoos in Japan. *Ibis* **131**: 94–98.
- Hoyt, O. F. (1979). Practical methods of estimating volume and fresh weight of bird eggs. *Auk* **96**: 73–77.
- Jourdain, F. C. R. (1925). A study on parasitism in the cuckoos. *Proc. zool. Soc. Lond.* **1925**: 639–667.
- Kornerup, A. M. & Wanscher, J. H. (1978). *Handbook of colour*. (3rd edn). London: Eyre Methuen.
- Lack, D. (1968). *Ecological adaptations for breeding in birds*. London: Methuen.
- Moksnes, A. (1992). Egg recognition in chaffinches and bramblings. *Anim. Behav.* **44**: 993–995.
- Moksnes, A. & Røskaft, E. (1987). Cuckoo host interactions in Norwegian mountain areas. *Ornis scand.* **18**: 168–172.
- Moksnes, A. & Røskaft, E. (1988). Responses of fieldfares *Turdus pilaris* and bramblings *Fringilla montifringilla* to experimental parasitism by the cuckoo *Cuculus canorus*. *Ibis* **130**: 535–539.
- 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. (1992). Responses of some rare cuckoo hosts to mimetic model cuckoo eggs and to foreign conspecific eggs. *Ornis scand.* **23**: 17–23.
- Moksnes, A., Røskaft, E., Bičík, V., Honza, M. & Øien, I. J. (1993). Cuckoo *Cuculus canorus* parasitism on *Acrocephalus* warblers in Southern Moravia in the Czech Republic. *J. Orn., Berl.* **134**: 425–434.

- Moksnes, A., Røskaft, E., Braa, A. T., Korsnes, L., Lampe, H. M. & Pedersen, H. C. (1990). Behavioural responses of potential hosts towards artificial cuckoo eggs and dummies. *Behaviour* **116**: 64–89.
- Moksnes, A., Røskaft, E. & Korsnes, L. (1993). Rejection of cuckoo (*Cuculus canorus*) eggs by meadow pipits (*Anthus pratensis*). *Behav. Ecol.* **4**: 120–127.
- Nakamura, H. (1990). Brood parasitism by the cuckoo *Cuculus canorus* in Japan and the start of new parasitism on the azure-winged magpie *Cyanopica cyana*. *Jap. J. Orn.* **39**: 1–18.
- Rothstein, S. I. (1990). A model system for coevolution: avian brood parasitism. *A. Rev. Ecol. Syst.* **21**: 481–508.
- Seel, D. C. (1977). Migration of the northwestern European population of the cuckoo *Cuculus canorus*, as shown by ringing. *Ibis* **119**: 309–322.
- Southern, H. N. (1954). Mimicry in cuckoos' eggs. In *Evolution as a process*: 219–232. Huxley, J. S., Hardy, A. C. & Ford, E. B. (Eds). London: George Allen & Unwin.
- Thomas, C. J., Thompson, D. B. A. & Galbraith, H. (1989). Physiognomic variation in dotterel *Charadrius morinellus* eggs. *Ornis scand.* **20**: 145–150.
- Tysse, T. (1993). [*Selection for blue eggs in the cuckoo, Cuculus canorus.*] Cand. scient. thesis, University of Trondheim. [In Norwegian.]
- Wasenius, E. (1936). Om de i Finland funna typerna av gökäggs och deras geografiska utbredning. *Ornis fenn.* **13**: 147–153. [In Finnish.]
- Wyllie, I. (1981). *The cuckoo*. London: Batsford.
- Yamagishi, S. & Fujioka, M. (1986). Heavy brood parasitism by the common cuckoo *Cuculus canorus* on the azure-winged magpie *Cyanopica cyana*. *Tori* **34**: 91–96.