



How do cuckoos find their hosts? The role of habitat imprinting

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ABSTRACT

Although a number of hypotheses have been proposed for how European cuckoo, *Cuculus canorus*, females may find hosts belonging to their foster parents' species, clear evidence is lacking for any of them. Here, we propose 'habitat imprinting' as an alternative mechanism for host selection and provide evidence that cuckoos are able to remember acquired information about a familiar habitat. We hand-reared seven cuckoos in one of five different artificial habitats and tested them as adults in habitat choice experiments. In each test habitat, a pair of zebra finches, *Taeniopygia guttata*, was presented as 'hosts'. We tested cuckoos of both sexes because the genotype of males may influence egg colour, and therefore egg mimicry; alternatively, habitat imprinting may be a general mechanism existing in both sexes but affecting egg mimicry only via females. Test cuckoos spent significantly more time looking at their respective familiar habitats than at other habitats in 1 of 2 test years. How long cuckoos were reared in the artificial habitats correlated positively with how long they spent in this habitat during the choice experiments. Additionally, test cuckoos remained longer with zebra finches that showed more nest-building behaviour but had lower levels of general activity, and they also observed these 'hosts' more frequently. If cuckoos choose to breed in habitats resembling those on which they were imprinted and search randomly for hosts in these habitats, they would increase their probability of parasitizing nests of their foster species. We propose that host specificity would be strengthened, however, if cuckoos use a sequence of several mechanisms, rather than just one, to find their hosts.

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Adaptations and counteradaptations of avian brood parasites and their hosts are important paradigms of coevolution (e.g. Rothstein 1990). Hosts have developed different means of egg rejection as adaptation against parasitism (e.g. Davies & Brooke 1988). The egg mimicry shown by some brood parasites is a counteradaptation to this behaviour (Brooke & Davies 1988; Rothstein 1990). Egg mimicry in European cuckoos, *Cuculus canorus*, is particularly surprising because this brood parasite is a generalist using a wide range of host species. Cuckoo eggs have been found in nests of more than 100 different species. Eleven main host species and a similar number of secondary ones have been identified (Wyllie 1981). Egg colours and patterns differ greatly between these host species, and the cuckoo eggs vary accordingly (Brooke & Davies 1988; Moksnes & Røskaft 1995).

Field observations suggest that each female cuckoo parasitizes only one host species and lays eggs of only one type (reviewed in Wyllie 1981; Dröscher 1988). Four hypotheses have been proposed to explain how a cuckoo female finds the nests of 'her' host species: (1) inherited

preferences (Newton 1893); (2) host imprinting (cuckoo chicks are imprinted on their foster species; e.g. Lack 1968); (3) natal philopatry (cuckoos return to where they were born and choose a host randomly; Brooke & Davies 1991); (4) nest site choice (cuckoo females choose a group of host species with similar eggs and nest sites and search for nests at random within these groups; Moksnes & Røskaft 1995). In an experimental study, Brooke & Davies (1991) found no evidence supporting hypotheses 1 or 2. Hypothesis 3 has been supported by observations of philopatry in cuckoos (Seel 1977; Wyllie 1981). In favour of hypothesis 4, Moksnes & Røskaft (1995) found that 77% of all cuckoo eggs were found either in nests of the host species with a matching egg type, or of species with similar nest sites. However, hypothesis 4 does not propose a mechanism for how females should find 'groups of host species with similar eggs and nest sites', and is hence not fully comparable to the other three hypotheses.

Here we propose 'habitat imprinting' (hypothesis 5) as a mechanism in European cuckoos for finding an appropriate host. We assume that cuckoo chicks learn the characteristics of their habitat in which they grow up by an imprinting-like process. We further assume that such characteristics of the natal habitat are the predominant

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vegetation type and structure in the area around their nest such as reed beds, meadows or open bushland. For reproduction, we propose that cuckoos establish their home ranges in areas consisting mainly of a habitat that resembles the habitat they had experienced as nestlings. When they parasitize the hosts available in this habitat, there is an enhanced chance of encountering nests of the host species by which they were reared.

Hypotheses 1 and 2 would allow for a strong host specificity and hence a good egg mimicry. In contrast, hypotheses 3–5 would predict that the levels of host specificity and egg mimicry should be far from perfect, especially in heterogeneous environments where different host species live in close proximity. In accordance with this expectation, Moksnes & Røskaft (1995) found only moderate mimicry with only 30% of the eggs classified as good or perfect mimics in a study of 12 000 parasitized clutches of European passerines contained in museum collections.

To test whether habitat imprinting may be involved in the nest selection process, we performed preference experiments in a large indoor aviary with cuckoos that had been hand reared in various, artificial habitats. We tested both male and female cuckoos, as the genotype of both sexes may influence the egg colour of daughters. In this case, egg mimicry could evolve only if cuckoos mate assortatively with males carrying genes for the same egg type. Habitat imprinting has been proposed as a mechanism that may lead to assortative mating (Southern 1954; Wyllie 1981). Alternatively, habitat imprinting may be a general mechanism in cuckoos perhaps serving a different purpose, but affecting egg mimicry only via females.

METHODS

Experimental Rearing Conditions

We collected seven cuckoo chicks in their nests (three females and two males in 1992, two females in 1993) from reed warbler, *Acrocephalus scirpaceus*, and marsh warbler, *A. palustris*, hosts 6–8 days after hatching (i.e. before their eyes opened). They were hand-reared for periods of 28–53 days in one of five artificial ‘habitats’ (Fig. 1): boxes (35 × 40 × 35 cm) lined with cardboard of highly contrasting colours on which were mounted structures that differed in shape, colour and material. The chicks remained in their natal nests which were mounted on a flowerpot in the middle of the box, allowing them to see the surrounding structures. The following ‘habitats’ were used: pink plastic balls on white (habitat $H_{O/H}$); blue ribbons on yellow ($H_{L/P}$); pine cones on red (H_N); commercial wicker nests as used for breeding zebra finches, *Taeniopygia guttata*, on green (H_F); and natural spruce branches on violet background (H_I). The strong differences were chosen to facilitate the cuckoos’ recognition of specific habitats, even if they perceive their environment using different criteria from ours. Furthermore, we aimed to avoid structures that might have been part of an innate preference mechanism of the cuckoos.

After the chicks fledged, we transferred them to cages (0.7 × 0.7 × 1.20 m) containing the same structures and

coloured cardboard as before and some branches and twigs to perch on. The cardboard was mounted on three sides and on the bottom of the cages, and the structures were distributed all over the cages, hanging from the top, attached to the sides and to the twigs. The young cuckoos were kept in these cages until independence. The cuckoos were exposed for different periods to the artificial habitats (see Table 1), as the age at independence varied between individuals. Then cuckoos were moved to indoor aviaries (17 m³) containing only twigs and branches for perching and various ground covers, but lacking the artificial habitat structures that had been used during imprinting. In summer, the birds could move freely between the indoor and outdoor aviaries (12 m³) which were surrounded by trees and buildings. Here the cuckoos were kept until the experiments, between the different test series and between the years of experiments. After the experiments the birds were kept in captivity for further behavioural studies, since they were probably unable to migrate or survive successfully in the wild.

Choice Tests

The seven cuckoos were tested for their habitat preferences at the age of 1 year. Cuckoos are known to reproduce in their first year (Seel et al. 1981; Dröscher 1988), but some may not start until 2 years of age (Glutz von Blotzheim & Bauer 1980). Therefore, we tested the five cuckoos reared in 1992 again in 1994. The choice experiments were performed in an experimental hall of 10 × 9 × 10 m with a Plexiglas ceiling providing natural daylight from above.

The five rearing habitats and one habitat made of reed stems representing the natal habitat of all experimental birds were presented simultaneously to each cuckoo (Fig. 1). Habitats were arranged in a circle around a ‘neutral’ zone in the centre providing food and water on the ground, three perches (one 3 m high and two 2 m high) and a cage in which the cuckoos were initially habituated to the experimental set-up (see Fig. 1). When sitting on the poles or anywhere else in the neutral zone the cuckoos could not see any of the experimental habitats (each 2 × 2 × 1.4 m), which were separated from each other and from the central area by opaque screens 2.6 m high. During their egg-laying phase, cuckoo females are known to sit in trees for extensive periods while watching potential hosts and nests (e.g. Wyllie 1981). The experimental set-up allowed similar behaviour to occur and for us to use this as a choice criterion: in front of each habitat we placed a perch 3 m high, allowing the cuckoo to watch the habitat from above. A bird sitting on this perch could see only this habitat and the other perches, but not any other habitats. Each habitat contained an artificial, open cup-shaped nest with one zebra finch egg and a cage with a pair of zebra finches, *T. g. castanotis*, to represent potential hosts. We chose zebra finches to exclude the possibility that an innate host preference may superimpose on potential habitat preferences and because this species shows reliable and frequent nest-building behaviour in small cages. Also, zebra finches are not disturbed

Table 1. Total time cuckoos spent in different habitats in the three test series, excluding sunshine hours

Date	Days of trial	Bird	Sex	Age (years)	Rearing habitat	Days in rearing habitat	Time spent in habitat (min)						Time in centre (%)
							H _I	H _F	H _{L/P}	H _{O/H}	H _N	Reed	
1993													
2-9 August	6	I	F	1	H _I	42	581	240	192	95	136	254	44.7
28 June-5 July	7	F	F	1	H _F	49	103	169	144	<u>208</u>	37	155	75.2
21-27 July	6	L	M	1	H _{L/P}	49	214	184	545	343	159	277	36.3
11-18 July	7	O	M	1	H _{O/H}	53	234	121	80	523	60	71	66.6
10-16 August	6	N	F	1	H _N	34	<u>60</u>	2	45	5	11	21	95.0
1994/1													
7-11 May	4	I	F	2	H _I	42	552	89	137	247	138	74	39.8
23-27 May	4	F	F	2	H _F	49	<u>180</u>	97	131	<u>635</u>	100	103	39.6
2-6 May	4	L	M	2	H _{L/P}	49	194	67	46	72	241	176	58.6
18-23 May	4	O	M	2	H _{O/H}	53	97	176	<u>382</u>	164	<u>153</u>	110	52.3
13-17 May	4	N	F	2	H _N	34	89	7	5	13	15	131	88.1
29 May-2 June	4	H	F	1	H _{O/H}	28	<u>174</u>	38	76	71	82	72	75.4
3-7 June	4	P	F	1	H _{L/P}	28	<u>488</u>	405	187	156	247	291	23.8
1994/2													
19-23 June	4	I	F	2	H _I	42	310	279	273	<u>597</u>	165	247	19.1
7-11 July	4	F	F	2	H _F	49	3	4	9	82	0	15	94.1
13-17 June	4	L	M	2	H _{L/P}	49	146	<u>241</u>	50	<u>199</u>	167	123	52.3
2-5 July	4	O	M	2	H _{O/H}	53	8	4	99	6	6	5	94.1
26-30 June	4	N	F	2	H _N	34	5	8	<u>67</u>	<u>104</u>	10	21	88.8
12-16 July	4	H	F	1	H _{O/H}	28	1	97	40	<u>5</u>	4	66	89.5
17-21 July	4	P	F	1	H _{L/P}	28	97	<u>195</u>	214	182	113	<u>235</u>	50.1

Bold and underlined numbers represent the familiar and the most frequently chosen habitats, respectively.

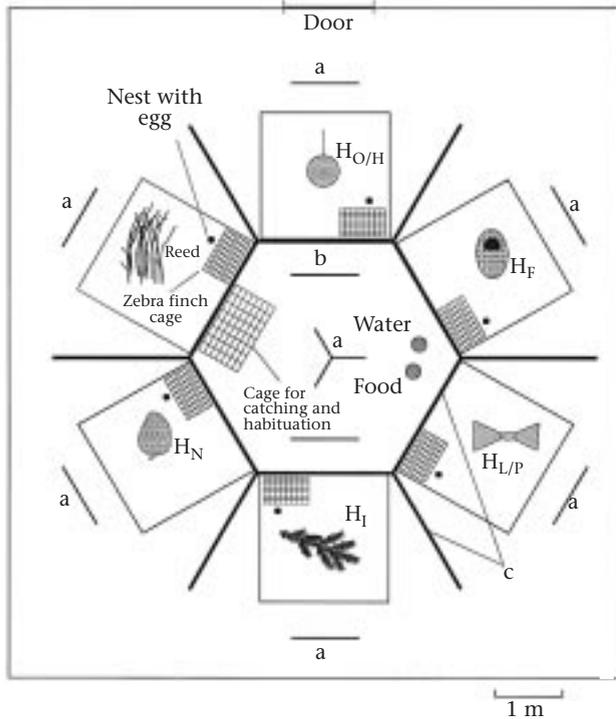


Figure 1. Experimental set-up: six test habitats (2×2 m and 1.4 m high) arranged around a 'neutral' area in the centre; a: perches 3 m high; b: perches 2 m high; c: opaque screens 2.6 m high; different symbols in the habitats represent the structures used.

by the presence of an observant cuckoo, probably because they lack a common evolutionary history.

We started the experiments when the cuckoos began calling, that is, were reproductively motivated. They were tested separately one after another. A bird was transferred from the holding aviaries into the cage in the neutral zone of the experimental hall in the early afternoon and released after 3–4 h of habituation. Recordings started at dusk the next morning. [Table 1](#) gives the dates and duration of the test series. In 1993, the cages with zebra finches were rotated between trials. In 1994, we did not change the experimental set-up between trials with different test birds, but did so between the two test series involving the same birds. The positions of the habitats and those of zebra finch cages were changed independently of each other to allow both position effects and individual 'host' preferences to be tested. After each individual test any eggs laid by the zebra finches were removed to ensure that the latter remained in the laying phase.

Behavioural Recordings

The cuckoo's position was continuously recorded from above by a video camera mounted in the ceiling of the experimental hall. We recorded activity by direct observation through one-way mirrors. The observation periods corresponded to periods when egg laying and male–female interactions were most common in wild cuckoos ([Wyllie 1981](#); personal observation; 1993: 2 h in the

morning, 1 h at noon, 2 h in the evening; 1994: 3 h starting from sunrise, 2 h in the evening). In 1994, we also recorded head and body postures of test cuckoos. Head postures recorded were either inclined to the left or right, looking up or down or turned to the left or right, whereas body posture was described as alert, normal, or with ruffled feathers. Postures and location were recorded once every 30 s.

We recorded the behaviour of each pair of zebra finches for 5 min twice a day directly before or after the cuckoo observation period to be able to check for a possible influence of zebra finch behaviour on the test cuckoo. Male and female pair members were observed in turn, each continuously for 30 s each. As a measure of activity, we noted the number of changes in position. We quantified nest-building behaviour as the number of times a zebra finch entered the nest with nesting material in its bill.

Analyses

From the continuous video recordings, we analysed the positions of test cuckoos for the total time between the first change of position at dawn and the last change at dusk. The time spent on the night roosts was not included in the analyses. For the habitat preference tests we used only the data from 1993 and those of the first test series in 1994, because in the second test series in 1994 four of seven cuckoos spent most of their time in the neutral area (>88%; see [Table 1](#)). This coincided with the onset of moult and reduced calling activity in several birds, suggesting that these birds were in a nonreproductive stage. In experiments 1993 and 1994/1 one very inactive bird also spent most of its time in the neutral area (95% and 88%, respectively; bird 'N' in [Table 1](#)). It was omitted from the habitat preference tests, because it was doubtful whether its occasional presence in one of the test habitats would give a reliable preference measure.

The habitat preference tests were analysed separately for the years 1993 and 1994 because of differences in the experimental procedure. The cuckoos tested in 1993 were hand reared for longer periods than those tested in 1994, which meant a longer exposure to the rearing habitat. In 1993, the experimental habitats were rearranged randomly between subsequent tests, whereas in 1994 they were rearranged only once between the two test series with the same birds. Additionally, the birds were exposed to external stimuli that varied between years, including sunlight (see the significant preference for sunlit perches reported below), and acoustic disturbance by anthropogenic activities in the vicinity of the experimental hall.

We used both test series of 1994 to test for the effects of habitat position and sunlit perches. An analysis restricted to three birds that spent more than 40% of their time in the experimental habitats in both runs of 1994 revealed no preferences for specific positions in the experimental hall ([Ludwig's \(1962\) exact subgroup tau test, one tailed: \$K=3, N=6, NS\$](#)). However, the presence of sunlit perches significantly influenced the habitat choice of test birds (binomial test: $N=12$ experiments involving five birds,

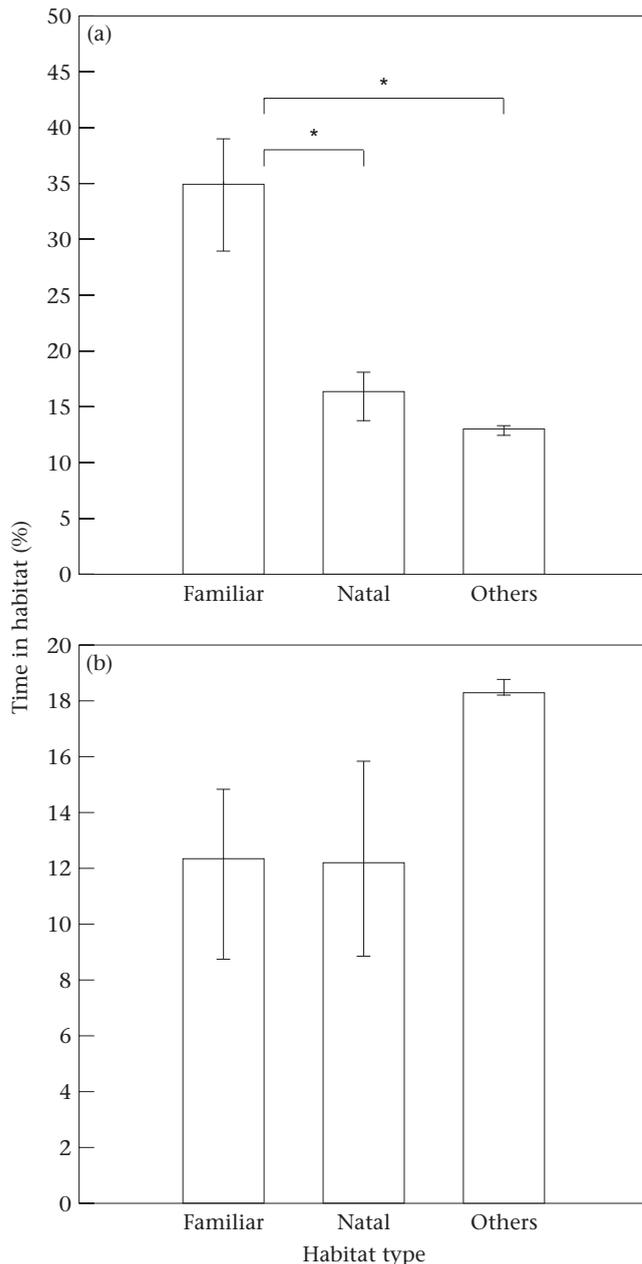


Figure 2. Time spent in the three habitat categories (a) in 1993 and (b) in 1994 (medians \pm quartiles). 'Familiar' is the habitat in which the cuckoos were reared; 'natal' is the natural reed habitat from which the cuckoos were taken; 'others' is for each bird the mean of the other four habitats in the test. * $P < 0.05$, see text.

$P < 0.001$). Therefore, we excluded from further analysis all hours of the test days when direct sunlight was shining into the experimental hall, that is, between 0945 and 1600.

From the behavioural recordings of cuckoo postures we classified different states. Here only the state 'potential attention towards zebra finches' is relevant. This combines all observations in which head postures allowed the test cuckoo to look at the zebra finch cage with one eye. We calculated the relative frequency of this state for each 'stay', one 'stay' being the time a cuckoo spent

continuously on a perch. In short stays the probability of observing any specific behaviour was low compared with longer stays. Therefore, we used only observations made in long stays (> 3 min) to check for relationships between cuckoo and zebra finch behaviour. The mean occurrence of 'potential attention towards zebra finches' in the different test cuckoos ranged from 39 to 62% of time during long stays.

For each individual cuckoo test period, we calculated the median zebra finch activity of all 5-min records made during this time. As nest-building behaviour of zebra finches was observed only rarely, we ranked the six zebra finch pairs according to the total number of observed nest-building behaviours for each of the two independent test series used for the habitat preference tests (1993, 1994/1).

Statistics

We used nonparametric statistics throughout, as the data differed significantly from normal distributions or the sample sizes were too small to test for deviations from normal distributions. We used two-tailed tests unless otherwise stated. We tested for habitat preferences by a Friedman two-way ANOVA by ranks. The rearing (=familiar) habitat is different for each cuckoo; therefore we tested for preferences of one of the three categories 'familiar', 'natal' and 'others', 'others' being the mean proportion of time spent in the four habitats other than the rearing and the reed habitat. For multiple comparisons between the single habitat types in 1993, we used an extension of the Quade test, a two-way ANOVA by ranks which gives more weight to animals that make a clearer choice between habitats (Conover 1980). For multiple comparisons, the Quade test has smaller type I and larger type II errors than the Friedman test and is therefore more conservative (Aldredge & Ratti 1986). For correlation analyses we used partly subgroup tau correlations: Torgerson's subgroup tau test (TSTT; Torgerson 1959; Lienert 1986), or for smaller data sets, Ludwig's exact subgroup tau test (LESTT; Ludwig 1962; Lienert 1986). These tests allowed us to calculate an overall relationship between the tested variables for all cuckoos, using several subgroups of the data set.

RESULTS

Preference for Rearing Habitat

The time spent in a particular habitat was used as an indicator of habitat preference. In the 1993 test series, the test cuckoos stayed significantly longer in their respective familiar habitats than expected by chance (Friedman two-way ANOVA: $K=3$, $N=4$ (two males, two females), $P < 0.05$; Fig. 2a, Table 1; multiple comparisons Quade test, familiar–other: $P < 0.05$; familiar–natal: $P < 0.05$; other–natal: NS). No preference was detected in test series 1 of 1994 (Friedman two-way ANOVA: $K=3$, $N=6$ (two males, four females), NS; Fig. 2b); only one out of six cuckoos spent most time in its familiar habitat (Table 1).

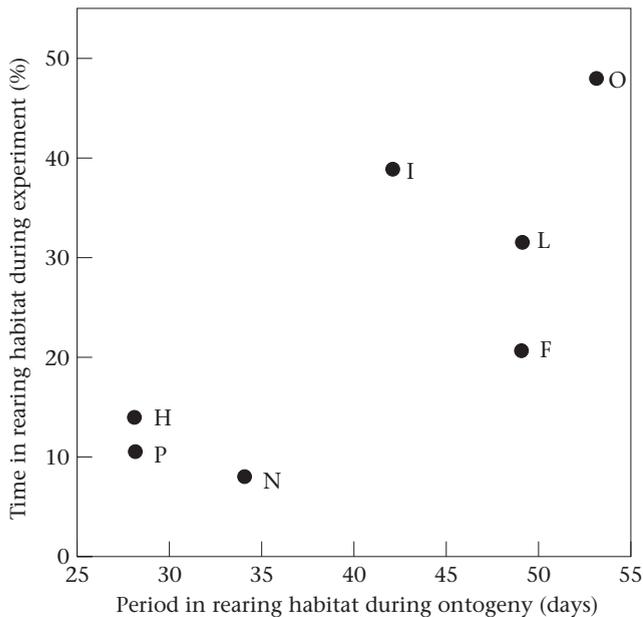


Figure 3. Relationship between the length of the imprinting period and habitat choice. The letters stand for the individual cuckoos.

Duration of Imprinting Period and Habitat Preferences

One important characteristic of imprinting is the existence of a sensitive period, a restricted period during which the animal establishes an attachment to the imprinting object (reviewed in Bolhuis 1991). If cuckoos learn their 'natal' habitat by such a mechanism the timing or the total length of exposure to the respective habitats should influence their later habitat preference. In our experiments the ages of independence and hence the lengths of the imprinting period varied between cuckoos. Cuckoos that had been exposed to their familiar habitat for longer periods spent significantly more time in this habitat during the experiment when tested at 1 year of age (Spearman rank correlation analysis, one tailed: $r_s=0.76$, $N=7$, $P<0.02$; Fig. 3). The data do not allow us to distinguish between an effect of the length of exposure and a possible limited sensitive period occurring only very late in the rearing period.

Influence of Activity of 'Hosts'

Cuckoos may prefer nests with low host activity, as this may indicate that a nest is currently unattended. Alternatively, cuckoos may observe nests with very active hosts more often because these are easier to detect. In 1993 and 1994, there was no significant correlation between median zebra finch activity and the proportion of time a cuckoo spent in the respective habitats if all cuckoos were combined (TSTT: 1993: $K=4$, $N=6$, $P=0.58$; 1994/1: $K=6$, $N=6$, $P=0.82$). However, host observation is mainly important for cuckoo females. In 1993, the two females tested spent more time in habitats with less active zebra finches (LESTT: $K=2$, $N=6$, $P=0.05$), while there was no significant relationship in 1994 (TSTT: $K=4$, $N=6$,

$P=0.78$). Cuckoos looked relatively more often in the direction of less active zebra finches (TSTT: $K=5$, $N=6$, $P=0.03$). This correlation was not significant for females alone (LESTT: $K=3$, $N=6$, NS).

Influence of Nest Building by 'Hosts'

Field observations suggest that cuckoos may find nests for later egg deposition during the nest-building stage (Chance 1922, 1940). Altogether, test birds did not spend more time near zebra finches that showed more nest-building behaviour (TSTT, one tailed, 1993: $K=4$, $N=6$, $P=0.46$; 1994/1: $K=6$, $N=5$, NS). Only females in 1994 tended to spend more time in habitats in which zebra finches performed nest building more often (TSTT, one tailed: $K=4$, $N=6$, $P=0.056$). Cuckoos looked more often towards active nest-building zebra finches (TSTT, one tailed: $K=5$, $N=5$, $P=0.05$). Females alone showed no significant relationship (LESTT, one tailed: $K=3$, $N=5$, NS).

Reproductive Motivation of Cuckoos

In 1993, the two males and one of the females were heard calling in their aviary during the experiments, which suggests that they were reproductively motivated. In 1994, all 2-year-old birds and a 1-year-old female called in the aviary and in the experimental hall. As the majority of the calls in the hall were given in the central area, we could not test statistically whether specific habitats were preferred for calling. The taking of host eggs, another potential indicator of reproductive interest in cuckoos, occurred once (female P, habitat H_F).

There was a positive correlation between the total time spent in a habitat during the whole test period and the proportion of time the test cuckoo observed the zebra finch pair in that habitat (TSTT: $K=5$, $N=6$, $P=0.003$; Fig. 4). When tested for females alone, the correlation was also significant (LESTT: $K=3$, $N=6$, $P=0.001$). This may suggest that cuckoos spent more time in certain habitats because of reproductive interest.

DISCUSSION

Evidence for Habitat Imprinting

The habitat preferences found in 1993 indicate that cuckoos were able to remember the habitat in which they had been reared. Early experience in a particular environment determines subsequent habitat preferences in several bird species and can even reduce or change genetic preferences for specific habitats (Klopfer 1963, 1965; Grünberger & Leisler 1990, 1993b). In our experiments, males and females did not differ in their preferences for the familiar habitat, suggesting that this may be a general mechanism in cuckoos as well. It may be responsible for the maintenance of egg mimicry only via the female sex, or via both sexes if the genotypes of males influence their daughters' egg phenotypes.

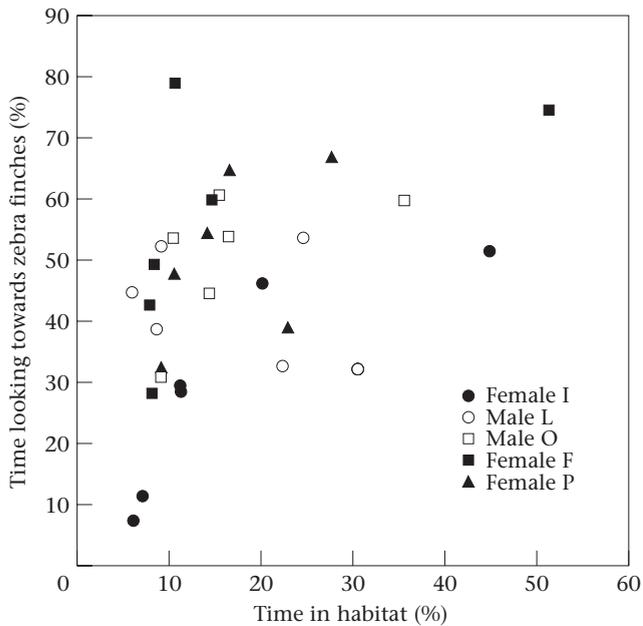


Figure 4. Relationship between the percentage of total time cuckoos spent in a habitat during the 1994/1 test series and the mean percentage of time they spent looking in the direction of zebra finches in that habitat.

When the cuckoos were tested again in 1994, they did not spend most of the time in their respective, familiar habitats as in the previous year. There are several possible explanations for this discrepancy. (1) Experience may change habitat preferences, especially if the habitat learned early in life is poorly structured (Hildén 1965; Glück 1984; Grünberger & Leisler 1990). (2) Habitat preferences may need to be reinforced in the first year to prevent forgetting of the learned habitat features. In several bird species, reproductive success and experience with a locality or habitat in previous nesting attempts can influence habitat choice (Sargent 1965; Catchpole 1972) and breeding site fidelity in subsequent nesting attempts (e.g. Greenwood & Harvey 1982; Oring et al. 1983; Bollinger & Gavin 1989). (3) The variation in experimental procedure between years, especially the time spent in the rearing habitat, might have caused the birds to react differently. This possibility is supported by the fact that the two yearlings in 1994, which had been reared for shorter periods in their experimental habitats than all other birds, did not prefer their familiar habitats. The positive correlation between the length of the imprinting period and the subsequent preference for the familiar habitat (Fig. 3) supports the hypothesis of habitat imprinting in cuckoos, but it may require a longer period than we allowed for the two chicks tested in 1994. This result may suggest that, like other birds, wild cuckoo chicks learn the characteristics of their habitat mainly after fledging (Sargent 1965; Catchpole 1972; Glück 1984), which is after 17–24 days (Wyllie 1981). After fledging, young cuckoos remain dependent on their foster parents for about 2 weeks but begin to explore the nest vicinity, whereby they may increase their knowledge of their natal habitat.

A preference for staying in a habitat does not necessarily mean that a cuckoo female would also choose this habitat for egg laying. However, in linnets, *Acanthis cannabina*, a preference for staying in an experimental, familiar habitat correlated with a preference for nesting there (Glück 1984). In our experiments, the cuckoos indicated reproductive motivation: they called and one female ate an egg. Also, the cuckoos clearly reacted to zebra finch behaviour which suggests that they regarded them as potential hosts. The time spent in a habitat correlated positively with the proportion of time zebra finches were observed by the respective cuckoos. Cuckoos observed zebra finches more often if they showed more nest building and less general activity. Additionally, in 1993 the two females tested spent significantly more time in habitats with less active zebra finches and in 1994, females tended to spend more time in habitats with nest-building zebra finches. These results suggest that (1) potential host nests at which there is less general activity are more attractive to cuckoos, perhaps because this would indicate reduced host attentiveness (parasitic eggs are more likely to be rejected if the host observes the cuckoo laying in its nest, e.g. Davies & Brooke 1988), and (2) female cuckoos preferentially observe nests in the nest-building stage probably because this may facilitate the optimal timing of parasitism.

If cuckoos preferred to stay and thereby gain information in habitats that appear familiar to them, this would increase the chance of detecting and parasitizing hosts in those habitats. Such a preference could arise as a result of a neophobic avoidance of strange habitats, which has been suggested to be an important component of habitat selection (e.g. Grünberger & Leisler 1993a). Linnets, when given the opportunity to see the familiar habitat, reduced their heart beat frequency (Gassman 1991), suggesting that these birds felt more 'secure'.

Comparison of Hypotheses

The evolution of egg mimicry requires a certain degree of host specificity. This is possible if cuckoo females lay the majority of eggs in nests of the host species that reared them. Indeed, using radiotelemetry, individual females were found to lay eggs in nests of only one species; a few eggs were laid in nests of a congener (Wyllie 1981; Dröscher 1988; unpublished data). Also, cuckoos seem to avoid host species that are unsuitable for rearing cuckoo chicks (Moksnes & Røskaft 1995). The pros and cons for each potential nest selection mechanism (except habitat imprinting) that may lead to host specificity have been discussed in detail by Brooke & Davies (1991) and Moksnes & Røskaft (1995). However, the following brief comparison shows that in each case, either supporting evidence for the mechanism is lacking or the mechanisms are not specific enough to lead to host specificity, at least in fragmented landscapes.

Philopatry

Wyllie (1981) found only four out of 60 birds (6.7%) as adults in the same area where they had been marked as

nestlings. This proportion is very low, even if mortality is assumed to be high. Seel (1977) found 32% of cuckoos recovered as adults that had been ringed as nestlings within 20 km, and 55% 21–200 km, from the nests in which they had been reared (recoveries within the breeding season from April to July only, $N=31$). While such a rather imprecise philopatry may account for a certain degree of host specificity in large areas of uniform habitats (Brooke & Davies 1991), it is probably not sufficient to maintain egg mimicry in today's fragmented landscapes.

Habitat imprinting

Our study provides evidence for habitat imprinting, even though it showed clearly in only 1 of 2 test years. Our preliminary field data of cuckoo females fitted with radiotransmitters are compatible with the habitat-imprinting hypothesis but data collection and the analyses have not yet been completed. If habitat imprinting were the only mechanism for finding host nests, cuckoos would search randomly for host nests in their natal habitat. In many cases they would end up laying their eggs in nests of the most abundant and/or conspicuous host of this particular habitat, which would also be, with increased probability, the species by which they were reared. Still, errors could occur frequently, especially in highly structured habitats where many potential host species may coexist, or if the abundance or conspicuousness of hosts differs between areas containing the same habitat type. The observation that egg mimicry is better in areas with homogeneous than with fragmented habitats (Moksnes & Røskaft 1995) supports the habitat-imprinting hypothesis.

In comparison with natal philopatry, a mechanism such as habitat imprinting would maintain egg mimicry and allow young cuckoos to disperse and colonize areas with fewer cuckoos and less competition for hosts. Under natal philopatry, dispersal would probably be maladaptive.

Host preference

No evidence was found for a host preference, either inherited or imprinted, in an experimental study by Brooke & Davies (1991), but their test series had small sample sizes as well. In comparison with the other proposed mechanisms of finding hosts, a host preference could result in very good egg mimicry. However, the analyses of Moksnes & Røskaft (1995) render it unlikely that cuckoos have perfect knowledge of 'their' host species and strictly lay their eggs in nests of this species. Evidence provided by Baker (1942) could point towards host preference. His observations suggested that females with overlapping territories may parasitize different host species.

Nest site selection

It is unclear whether and how nest site selection could maintain egg morphs. Moksnes & Røskaft (1995) found

that 77% of cuckoo eggs were in nests of hosts with nesting sites similar to those of the main host but (1) they did not propose a mechanism for how females could recognize or detect 'similar nest sites' and (2) for the data analyses, they defined very coarse categories of similarity, such as nest sites in trees, nest sites in low vegetation, nest sites on the ground and nest sites in holes. It appears unlikely, for example, that a preference of cuckoos for nest sites in low vegetation could contribute much to the maintenance of egg morphs, as 42 of the parasitized bird species examined in Moksnes & Røskaft's study nest exclusively or partly in low vegetation but their eggs correspond to a wide range of different cuckoo egg types.

A Hierarchical Decision Process for Nest Selection

The above discussion suggests that a single mechanism maintaining different egg morphs within a population is unlikely. A solution to this problem could be a stepwise decision process that combines several of the hypothesized selection mechanisms in a sequence. (1) On their spring migration from the African wintering grounds, cuckoos return approximately to the geographical region where they were born by using an innate or learned migration route (natal philopatry). This enhances the probability that they encounter their natal habitat type. (2) Cuckoos search for a habitat that they had been imprinted on as nestlings or fledglings. (3) Within this habitat they search for suitable nests. For that purpose, they may use finer selection criteria such as gross characteristics of the host species or of the microhabitat around the nest which they might have learnt when young. This assumed temporal sequence of decision processes is paralleled by a spatial hierarchy from broad to fine scale. Sequential and spatially hierarchical decisions have also been proposed as the central mechanism in habitat selection of nonbreeding migratory land birds (Hutto 1985) and of raptor species (Gamauf 1988).

The relative importance of habitat (step 2) versus potential finer microhabitat and/or host characteristics (step 3) for nest selection may be tested in an area containing at least two distinct habitats, each of them inhabited by a host that is specialized in one of them, and by a host species that uses both habitats alike (generalist).

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