



## Cuckoo females preferentially use specific habitats when searching for host nests

WOLFGANG VOGL\*, MICHAEL TABORSKY†, BARBARA TABORSKY\*, YVONNE TEUSCHL\* & MARCEL HONZA‡

\*Konrad Lorenz-Institut für Vergleichende Verhaltensforschung (KLIVV), Austrian Academy of Sciences

†Department of Behavioural Ecology, Institute of Zoology, University of Bern

‡Institute of Landscape Ecology, Academy of Sciences of the Czech Republic

(Received 14 April 2001; initial acceptance 28 June 2001;  
final acceptance 20 April 2002; MS. number: 6897)

Egg mimicry is an important adaptation of common cuckoos, *Cuculus canorus*, against rejection of eggs by their respective hosts. A precondition for the maintenance of egg mimicry is that female cuckoos find hosts with a matching egg type. Experimental evidence indicated that habitat imprinting may be important for host selection. We tested whether the spacing and laying patterns of female cuckoos in the field are compatible with the supposed habitat-imprinting mechanism. We observed 16 females, with the help of radiotelemetry; of seven females, we observed directly 26 egg layings and 27 nest visits without laying. As expected if females were imprinted on different vegetation types, (1) the distribution of vegetation types differed between female home ranges, (2) female habitat use differed from average habitat availability within the egg-laying area (habitat preference), (3) females visited nests and deposited their eggs in the habitat they preferred, and (4) females laid their eggs consistently in a particular habitat type, irrespective of the host species. These results indicate that cuckoo females show habitat preference when searching for suitable host nests. Hence our data are compatible with the habitat-imprinting hypothesis, but owing to the habitat specificity of hosts the data cannot disprove a potential role of host specificity in cuckoo females.

© 2002 The Association for the Study of Animal Behaviour. Published by Elsevier Science Ltd. All rights reserved.

The adaptations and counteradaptations of avian brood parasites and their hosts are a paradigm of coevolution (Dawkins & Krebs 1979; Davies & Brooke 1988; Davies et al. 1989; Rothstein 1990; Krebs & Davies 1993). Many cuckoo hosts have developed efficient means to detect and reject parasitic eggs (Rensch 1924; Davies & Brooke 1989a, b; Moksnes et al. 1991; Briskie et al. 1992; Soler et al. 1994; Lotem et al. 1995). As a consequence, cuckoo eggs mimic their hosts' eggs to some degree ('egg mimicry'; Latter 1902; Baker 1923; Chance 1940; Brooke & Davies 1988, 1991; Rothstein 1990; Moksnes & Røskaft 1995).

The common cuckoo, *Cuculus canorus*, is an obligatory brood parasite, using at least 125 species of European

passerines, of which 15 are parasitized regularly (Baker 1942; Lack 1968; Wyllie 1981; Moksnes & Røskaft 1995). Cuckoos are thought to exist in different subpopulations (gentes), each specialized on one specific host species (Newton 1893; Lack 1968; Wyllie 1981; Davies & Brooke 1988). There is genetic evidence that these gentes are restricted to female lineages (Gibbs et al. 2000). The eggs of host species differ greatly in colour and markings, however. So, if individual cuckoo females lay eggs with a colour pattern that matches the pattern of a particular host species, as suggested by recent data (G. Rudolfsen, A. Moksnes, E. Røskaft, O. Kleven, M. Honza, B. Taborsky, M. Taborsky, Y. Teuschl & W. Vogel, unpublished data), how do the females find the nests of this host?

Five hypotheses have been proposed to explain how female cuckoos find 'their' hosts with the matching egg type.

(1) Inheritance (Newton 1893). The host preference is genetically determined.

(2) Host imprinting (e.g. Southern 1954; Lack 1968; Brooke & Davies 1991). The young cuckoo learns the characteristics of its foster parents by an imprinting process either before or soon after fledging.

Correspondence: M. Taborsky, Department of Behavioural Ecology, Institute of Zoology, University of Bern, Wohlenschtrasse 50a, CH-3032 Hinterkappelen, Switzerland (email: michael.taborsky@esh.unibe.ch). W. Vogl and B. Taborsky are at KLIVV, Savoyenstrasse 1a, A-1160 Wien, Austria. Y. Teuschl is at the Zoological Museum, University of Zürich-Irchel, Winterthurerstrasse 190, CH-8057 Zürich, Switzerland. M. Honza is at the Institute of Landscape Ecology, Academy of Sciences of the Czech Republic, Kvetna 8, 60365 Brno, Czech Republic.

(3) Natal philopatry (Brooke & Davies 1991). Cuckoos return to the area where they were born and choose hosts randomly.

(4) Nest site choice (Wyllie 1981; Moksnes & Røskoft 1995). A cuckoo chooses 'a group of host species with similar eggs and nest sites, and searches for nests at random within this group' (Moksnes & Røskoft 1995). This hypothesis does not propose a mechanism for how nest sites are recognized, nor does it specify which characteristics of nest sites are used as cues for nest site choice.

(5) Habitat imprinting (Teuschl et al. 1994, 1998). Cuckoo chicks learn the characteristics of the habitat in which they grow up by an imprinting process and choose similar habitats later for egg laying. Such characteristics of the natal habitat could be the predominant vegetation type and structure in the area around their nests such as reedbeds, meadows or open bush. When they parasitize hosts living in this habitat, there is an enhanced chance of encountering nests of the host species by which they were reared, as potential hosts are usually habitat specific when breeding.

Teuschl et al. (1998) reviewed the existing evidence for hypotheses 1–4. None of them has been strongly supported by data. The fifth hypothesis, habitat imprinting, was tested in a laboratory experiment. Seven cuckoos were hand-reared in cages among one of five artificial 'habitats', structures that differed strongly between test birds in colour, shape and texture. As adults, these cuckoos were tested separately for habitat preferences in a simultaneous choice test. The results indicated that habitat imprinting may be an important mechanism determining the nest site choice of cuckoo females (Teuschl et al. 1998). However, evidence from the natural environment of cuckoos is still missing.

We investigated whether habitat imprinting may play a role in the choice of host nests by female cuckoos in the natural situation. In our study area several vegetation types were present. We hypothesized that if females had been imprinted on particular vegetation types, they should use vegetation specifically when searching for host nests. Assuming that not all cuckoo females living in a diverse and fragmented landscape grew up in the same vegetation type, four predictions can be derived from this hypothesis for the spacing and egg-laying behaviours of cuckoo females.

(1) Birds tested for a choice of laying habitats show a species-specific preference (e.g. Catchpole 1974; Glück 1984; Mazur et al. 1998); in contrast to this, the habitat preference of female cuckoos should vary between individuals.

(2) Female cuckoos should show a clear preference, that is they should use certain habitats more often than expected from the habitat distribution in the available egg-laying area.

(3) Such habitat preference should serve primarily to find the right nests, so nests should be visited and eggs should be laid mainly in these preferred habitats.

(4) A preference for laying habitats should lead to individual habitat consistency, so when laying successive

eggs, females should use nests in the same type of vegetation.

We emphasize that this type of study can distinguish clearly between habitat and host specificity only if hosts are not habitat specific. This is unlikely to be the case, however, as a habitat-imprinting mechanism can work only if hosts are habitat specific. Therefore, we did not aim to distinguish between these two possibilities, but to test whether cuckoo female behaviour reveals a habitat preference, which would be consistent with a habitat-imprinting mechanism.

We observed 16 cuckoo females extensively with the help of telemetry in a fish pond area with highly fragmented habitats (W. Vogl, B. Taborsky, M. Taborsky, Y. Teuschl & M. Honza, unpublished data). To test our predictions, we recorded the females' spatial and temporal usage of different vegetation types and observed their behaviour before and at egg laying.

## METHODS

### Study Site

All data were collected in Southern Moravia, Czech Republic, during four breeding seasons of cuckoos from 1995 to 1998 (May to beginning of July). The study area was comprised of a commercially used fish pond area with reed, herb and bush vegetation around the ponds, and forests consisting mainly of oaks in the vicinity. From three major habitats, 'forest', 'forest edges' and 'pond edges', cuckoos bred only in the latter (W. Vogl, B. Taborsky, M. Taborsky, Y. Teuschl & M. Honza, unpublished data).

This pond edge area consisted mainly of six vegetation types which we mapped with transects laid perpendicular to the shoreline of ponds and channels and 10 m apart. Each transect extended from the open water surface of a pond or channel to the next road, water surface or forest edge. We recorded the extent of each vegetation type along the transects, the proportions and heights of different plant species, and, if reed vegetation was present, also its age. Each vegetation type was named after the dominant plant species: 'reed' (mainly *Phragmites australis*), 'reed mixed with herbs' (maximum of 20% herbs), 'reed mace' (mainly *Typha latifolia*), 'herbs' (mainly *Solidago canadensis*), 'herbs mixed with nettles and grass' (minimum of 50% *S. canadensis*, *Urtica dioica* and different grass species, and with a maximum of 20% reed) and 'nettles' (mainly *U. dioica*). For statistical analyses of habitat preference we combined the vegetation types reed, reed mixed and reed mace into the category 'reed habitats' and the vegetation types herbs, herbs mixed and nettles into the category 'herb habitats'. Nests of reed warblers, *Acrocephalus scirpaceus*, and great reed warblers, *A. arundinaceus*, were abundant in the reed habitats. In the herb habitats, nests of marsh warblers, *A. palustris*, and sedge warblers, *A. schoenobaenus*, prevailed with some reed bunting, *Emberiza schoeniclus*, nests in certain areas. Hence in both vegetation categories within the egg-laying area, at least two potential host species were present,

which would help to distinguish habitat from host preference.

### Catching, Radiotracking and Data Recording

We caught 37 cuckoos (16 females and 21 males) with mist nests, banded them with an aluminium ring and a coloured wing tag (1.5 × 2.5 cm), and attached radio transmitters (18 × 7 × 3 mm; 2.5 g including battery, i.e. ca. 2.5% of female body mass). Transmitters were glued with cyanoacrylate to the upper side of the central tail feather, with the antenna tied alongside the feather so that the tag would fall off during the next moult at the latest. Birds were tracked at distances down to ca. 40 m (about 90% of time further away than that). Signals of two of the 16 tagged females were never detected (probably because of transmitter failures); all others were observed for various periods of time (with periods depending mainly on transmitter performance). We could not detect any effects of the transmitters on the behaviour of the birds, even though tagged birds were observed intensively and for extended periods. The birds were studied under licence issued by Okresni urad Hodonin, referat zivotniho prostredi (Czech Republic).

Five observers collected most of the data. Each observer followed continuously a particular focal bird in the major observation periods (continuous focal animal sampling: 1400–1900 hours for egg laying, early morning and late evening for intraspecific interactions). The observer tried to get a direct view of the target bird without disturbing it. If the bird could not be seen or its location was not detected exactly, cross bearings were taken to estimate its position. As long as the target cuckoo was seen or heard, its behaviour was recorded.

Telemetry fixes and locations identified by observations of radiotagged and wing-tagged birds were marked on maps with scale 1:10 000, together with date, time and, if known, behaviour of the bird. When egg layings or nest visits without egg laying were observed we noted the host species, the nest number, the habitat around the nest, the egg-laying duration and the behaviour of the target female and the hosts (if they were seen) before, during and after the egg laying.

### Data Analyses

From the maps, we digitized the locations, and calculated the range sizes of birds, with the software package 'Home' (developed and documented by H. Winkler & B. Taborsky, unpublished). We used an adaptive kernel estimator for determining ranges, which is based on a bivariate probability density function of independent locations (Worton 1987). For this purpose, we calculated the 'time to independence' (TTI) intervals for each cuckoo (i.e. the minimum time intervals at which two successive recordings revealed statistically independent locations; Swihart & Slade 1985) and used only locations recorded at intervals larger than TTI for our home range estimates. For a detailed account of this method see Taborsky & Taborsky (1992).

Of 2180 radio fixes obtained in total, 323 were determined as being statistically independent. From these, we were able to estimate home range sizes and locations of nine of the 16 telemetry females. We calculated the absolute and relative amounts of the six vegetation types in the egg-laying area of each home range of seven females that had been observed at egg laying.

Only the vegetation types within the pond edge habitat were included in the analyses of preferences, as all egg layings and nest visits occurred in these vegetation types. Generally the pond edge area was mapped in transects (see above). To get an area estimate, within each transect we mapped the length of each vegetation type and multiplied it by 10 to account for the 10 m between transects. For each mapped location of a bird the corresponding transect was determined, and the vegetation type that made up the major proportion of this transect was regarded as the vegetation type where the bird was sitting (in all cases included in the analyses the major vegetation type made up at least 70% of the transect's area).

### Test of Predictions

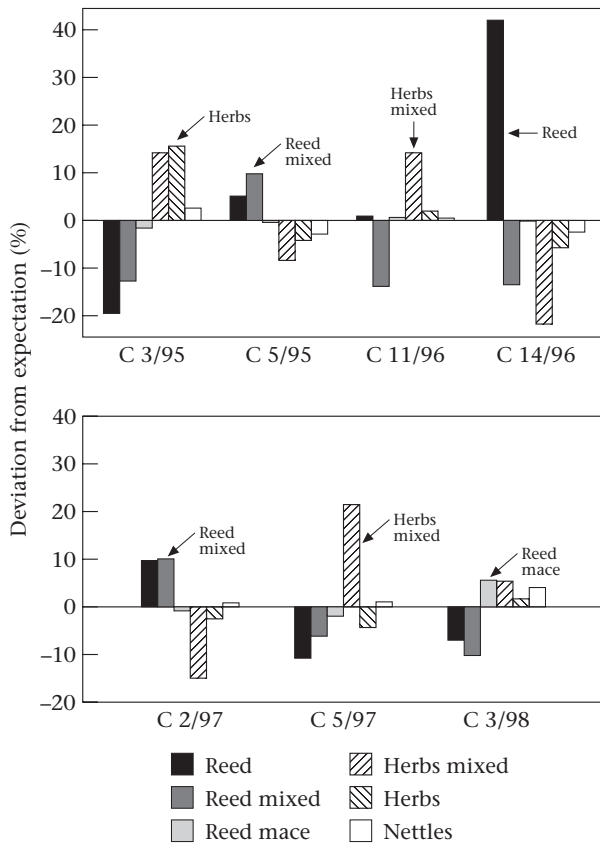
(1) We compared the proportions of the six vegetation types contained in individual home ranges with the expected proportions as derived from the total egg-laying area of all telemetry females combined.

(2) We compared the frequencies of observed independent locations (total  $N=154$ ) of seven cuckoo females in the reed and herb habitats with the expected distribution of observed locations if these habitats were used in proportion to their availability within the range covered by these females.

Female egg-laying areas consisted of different proportions of reed and herb habitats. For a test of prediction 3 we compared how often females laid an egg or just visited a nest in one of these two vegetation categories with (a) the proportion of the egg-laying area within the home range of this female that consisted of these habitats, and (b) the time this female spent in these habitats on egg-laying days (time spent in a vegetation type has been regarded as an adequate measure of habitat selection in birds; Glück 1984; Grünberger & Leisler 1993a, b).

To test prediction 4 we checked by direct observation of layings how many eggs each female laid in reed and herb habitats, and how consistently females used particular host species. We also checked whether there were other nests within the potential egg-laying area of the female that were in a state ready for parasitism on the day of laying, and we noted the area's vegetation type and host species. A nest was 'ready for parasitism' when one, two or three eggs were present. To ascertain this we checked nest sheet data provided by A. Moksnes & E. Røskaft (personal communication).

We used nonparametric statistics throughout, as data either deviated significantly from normal distributions or were not sufficient to test reliably for the underlying distributions. Two-tailed error probabilities are given throughout.



**Figure 1.** Distributions of vegetation types in the home ranges of seven female cuckoos. Each bar shows the deviation of a vegetation type in a home range from the proportion of this vegetation type within the entire area used by all females.

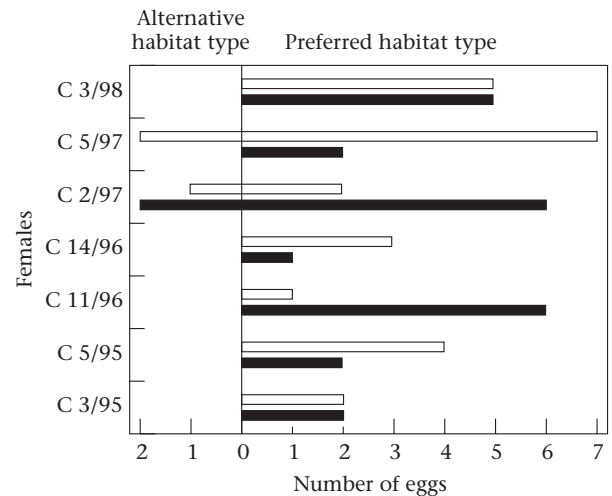
## RESULTS

### Prediction 1: Vegetation Type Differences

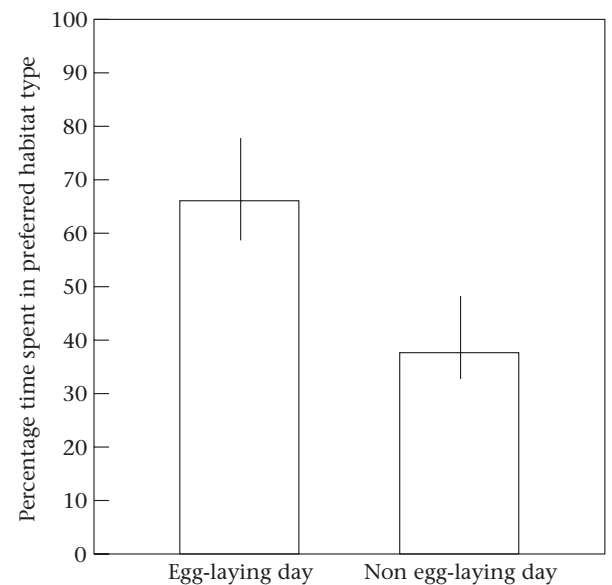
The distribution of the six vegetation types differed between female home ranges (Fig. 1). Four females showed the greatest positive deviations from expectation (distribution of vegetation types in all female home ranges combined) with vegetation types reed mixed and herbs mixed (two females each) and three females showed the greatest positive deviation with vegetation types herbs, reed and reed mace (one female each). Generally, there was a tendency for either reed habitats or herb habitats to be preferentially contained in a female's home range (see Fig. 1).

### Prediction 2: Habitat Preference

The distribution of observed locations of female cuckoos in reed and herb habitats differed significantly from an expected random distribution of locations in these habitats within the range used by these females (combining probabilities from seven independent Fisher's exact probability tests (Fisher 1954):  $\chi^2_{14}=40.92, P<0.001$ ). We consider habitat categories used more often than expected by a female to be preferred.



**Figure 2.** Numbers of eggs laid (■) and nest visits without egg laying (□) of seven females in host nests within the preferred habitat type and the alternative habitat type. Preference was derived from the time spent in a habitat type.



**Figure 3.** Average percentage of time females spent in the preferred habitat type, on egg-laying days and on days without laying. Bars represent medians ± quartiles.

### Prediction 3: Egg-laying Preference

Females visited nests and laid eggs almost exclusively in their preferred habitat category (reed or herb habitats, see 2 above; binomial tests:  $x=0, N=7$  females,  $P<0.02$  for nest visits and egg layings, respectively; Fig. 2). They also spent more time in these habitats on egg-laying days than on other days (Wilcoxon signed-ranks test:  $T=0, N=7$  females,  $P<0.02$ ; Fig. 3).

In 16 of 26 layings one or more alternative nests suitable for parasitizing were present within the female's pond edge area contained in her home range (29 nests in total). Of these alternative nests, 15 were in the same vegetation type as where the female laid and belonged to

**Table 1.** Vegetation types and host species of 26 egg layings and alternative nests available in the respective female's egg-laying area on the laying day

Female cuckoo	Eggs laid	Other nests
C 3/95	HMp	<b>Up, Up, Rs</b>
	HMp	HMp
C 5/95	RMp	<b>RMp, Ts</b>
	RM <sub>s</sub>	<b>RM<sub>s</sub>, Ts</b>
C 11/96	HMp	—
	HMp	—
	HMp	—
	HMp	<b>Rs</b>
	HMp	—
C 14/96	HMp	<b>Rs, Rs</b>
	Rs	—
C 2/97	Rs	Rs, Rs, Rs, Rs
	Rs	Rs, Rs, Rs
	HMsch	—
	Rs	Rs, Rs
	Rs	Rs, Rs
	Rs	—
	Rs	—
	HMsch	—
C 5/97	HMp	<b>Up, Rs</b>
	HMp	HMp
C 3/98	HMsch	<b>Rs</b>
	HMsch	<b>Rs</b>
	HMsch	—
	HMsch	<b>Ra</b>

Vegetation type: HM=herb mixed; U=*Urtica*; R=reed; RM=reed mixed; T=*Typha*. Hosts: p=*Acrocephalus palustris*; s=*A. scirpaceus*; sch=*A. schoenobaenus*; a=*A. arundinaceus*. **Bold** letters: vegetation types or hosts other than the ones used for laying.

the same host species, while 14 were either in a different habitat or belonged to a different host species, or both (Table 1). When nests were available in more than one habitat at a time, but in different numbers per habitat, one female (C 5/95) laid in the habitat containing the most nests, while three females (C 3/95, C 11/96<sub>(egg 6)</sub>, and C 5/97) laid in the habitat with the fewest nests. When nests of more than one host species were available at a time, but in different numbers, three females (C 3/95, C 5/95 and C 5/97) laid in nests of the most common host and one (C 11/96<sub>(egg 6)</sub>) laid in a nest of the rarest. The difference in choice of common and rare options between habitat and host categories was not significant (Fisher's exact probability test, two-tailed:  $N=8$ ,  $P=0.49$ ).

#### Prediction 4: Choice Consistency

All observed 26 egg layings and 27 nest visits of seven females occurred in the same general habitat, the 'pond edges' (W. Vogl, B. Taborsky, M. Taborsky, Y. Teuschl & M. Honza, unpublished data). One female was observed at only one laying. Five of the other six females laid all eggs in one of the two habitat categories (reed or herbs), and only female C 2/97 laid two of eight eggs in the other category (significant difference from random, binomial test:  $\chi=0$ ,  $N=6$  females,  $P<0.05$ ; Fig. 4). When more than one nest was available at a time in different habitats (10

layings of five females; see Table 1), eggs were always laid in the preferred habitat. The cumulative probability that this happened by chance was  $3.8 \times 10^{-4}$ . Host specificity was almost as high as habitat specificity, which was evident when nests of different hosts were available at the same time (eight layings of four females, cumulative probability that host specificity was a result of chance =  $5.2 \times 10^{-3}$ ; Table 1); only female C 5/95 laid her two eggs with different hosts, and female C 2/97 also laid two of her eight eggs with a different host (Fig. 4).

## DISCUSSION

The habitat-imprinting hypothesis assumes that females are imprinted on a particular habitat or vegetation type during ontogeny, which they use preferentially for reproduction when mature (Teuschl et al. 1998). Habitat imprinting and subsequent preference may be regarded as a general mechanism that is widespread in birds (e.g. Klopfer 1963; Glück 1984; Grünberger & Leisler 1990, 1993a, b), and nonrandom use of habitats has also been shown in other birds (e.g. in brood parasitic brown-headed cowbirds, *Molothrus ater*, Gates & Evans 1998). In our study on radiotagged adult cuckoo females, we found support for four predictions derived from the habitat-imprinting hypothesis.

First, the distribution of specific vegetation types that were relevant for cuckoo reproduction in our study area differed between individual female home ranges. Given that habitat distribution within home ranges is an indication of preference, this was expected because it is likely that the females had been reared in a range of different vegetation types. Second, within the egg-laying areas in the females' home ranges, the telemetry females preferred one habitat category (either reed or herb habitats) over the other. We measured habitat use by the number of observed, independent locations, which corresponds to time spent in a certain vegetation type and is a commonly used criterion for habitat preference (e.g. Klopfer 1963; Partridge 1974; Glück 1984; Morton 1990; Grünberger & Leisler 1993a, b). Third, females visited nests and parasitized hosts generally in their 'preferred' vegetation type, where they also spent more time on egg-laying days than on days without laying. Lastly, females were consistent with regard to habitat when laying two or more eggs successively. Of 25 eggs laid by six females, 23 met this criterion. In the only two cases where a female laid an egg in a different habitat (eggs 3 and 8 of female C 2/97), there were no nests available in her preferred habitat (Table 1).

These results suggest that cuckoo females have specific and consistent habitat preferences, which may differ between individuals. Unfortunately we do not know in which habitats the observed females had been reared. Owing to a high juvenile mortality and a low recapture rate of cuckoos (Seel 1977; personal observations), it is virtually impossible to capture and study the same birds as nestlings and in the adult stage, in representative numbers. Of 78 nestlings banded during this study, none was recaptured as an adult (M. Honza et al., unpublished data), even though 37 adults were caught in total within

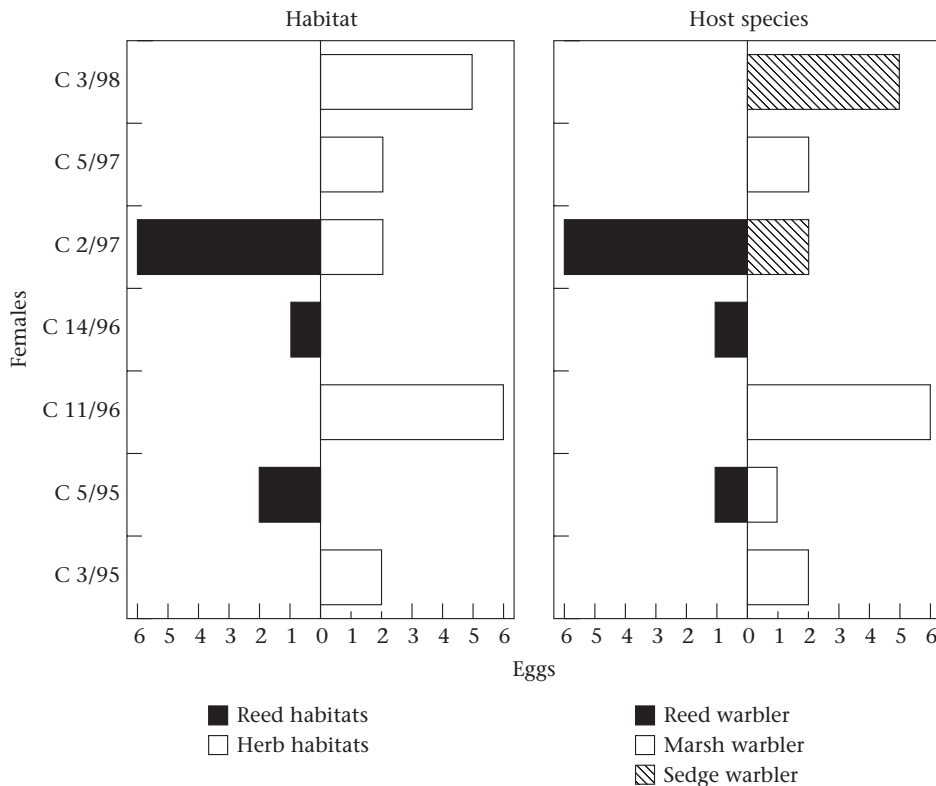


Figure 4. Eggs laid by each female in reed or herb habitats and in nests of the listed host species.

a period of 4 years. Therefore, our conclusion regarding individual differences relies on the assumption that it is likely that our radiotagged females had originated from nests in different vegetation types.

Habitat preference in the reproductive context is widespread in birds and has been shown for example in reed warblers (Catchpole 1974), linnets, *Acanthis cannabina* (Glück 1984), kiwis, *Apteryx australis* (Taborsky & Taborsky 1995), brown-headed cowbirds (Evans & Gates 1997) and barred owls, *Strix varia* (Mazur et al. 1998). Apparently it is also prominent in potential cuckoo hosts (Catchpole 1974) which is a precondition for a rather rough mechanism such as habitat imprinting to work in cuckoos, providing the necessary host specificity to allow for the evolution of egg mimicry. This habitat preference of hosts makes it difficult, however, to separate habitat from host preference in cuckoos. Four of the six females that we observed laying two or more eggs in succession deposited these eggs in the nests of only one host species.

When the telemetry females were surveyed during egg laying, other nests ready to be parasitized were available at the same time within the respective home ranges in 62% of cases. In 10 layings of five females a total of 14 nests were available in alternative habitats. However, in only four of these cases with nests in alternative habitats, did the host species not differ as well. Therefore, even though habitat preference appeared to be slightly greater than host choice when laying, this data set did not suffice to separate statistically between host and habitat preference, owing to low statistical power.

The abundance and distribution of potential host species differed strongly between the *Acrocephalus* species in our study area. In reed habitats, there were 5.4 times more nests of reed warblers than nests of great reed warblers and, correspondingly, seven of eight eggs laid in reed habitats were laid in reed warbler nests. There were about 1.3 times as many nests of marsh warblers than nests of sedge warblers in herb habitats (the information was not as good for these two species as for the other two; A. Moksnes & E. Røskaft, personal communication), and 10 of 17 eggs laid in herb habitats were laid in marsh warbler nests. Therefore, the distribution of cuckoo eggs between host species resembled closely the availability in our study area. This was also reflected in the cases where different numbers of nests per host species were available at the same time, when three of four females laid in the nest of the host that was more common.

Experimental evidence suggested a possible role of habitat in the host-finding process of cuckoos (Teuschl et al. 1998), while comparable evidence is lacking for a role of host species (Brooke & Davies 1991). If the cuckoo were strongly host specific one would expect perfect or very good egg mimicry. In contrast, from analysing museum collections Moksnes & Røskaft (1995) concluded that the European cuckoo is more of a generalist than previously thought, as they found a relatively low degree of 'host specialization' of cuckoos (44.3%). Similar conclusions were drawn from a study of the quality of egg mimicry at our study site in the field (Edvardsen 1998). A rather poor degree of egg mimicry would be expected if

only rough mechanisms such as habitat imprinting are the primary mechanism by which female cuckoos find appropriate nests to parasitize.

In conclusion, our study shows that the behaviour of free-ranging cuckoo females is consistent with the habitat-imprinting hypothesis. Owing to a high degree of habitat specificity of hosts our data cannot rule out an important role of hosts in the nest-finding process of cuckoo females, even though evidence from previous studies supported habitat imprinting rather than a direct host preference by imprinting or an innate template (Brooke & Davies 1991; Teuschl et al. 1998). For cuckoo females ready to lay there may be an important role of observing hosts directly, but at a later stage in the presumed hierarchical process of host finding (see Teuschl et al. 1998 for experimental evidence). Habitat imprinting is probably a general mechanism for the selection of habitats for feeding and for reproduction, not only in birds but probably also in mammals (see Olson & van Horne 1998; Wecker 1963) and insects (Thorpe 1939, 1945; the term 'habitat imprinting' was first used in this context). On the basis of such a general mechanism it may be a small step for the evolution of means ensuring that cuckoo females find the right hosts, which is a precondition for the evolution of egg mimicry.

### Acknowledgments

We are indebted to Katharina Förster, Oddmund Kleven, Oldrich Mikulica, Arne Moksnes, Eivin Røskaft and Geir Rudolfson for help in the field and with the logistics in this study. We are particularly grateful to Arne Moksnes and Eivin Røskaft for access to unpublished host nest data. This study was supported by the Austrian and Czech Academies of Sciences.

### References

- Baker, E. C. S. 1923. Cuckoo's eggs and evolution. *Proceedings of the Zoological Society*, **19**, 277–294.
- Baker, E. C. S. 1942. *Cuckoo Problems*. London: Witherby.
- Briskie, J. V., Sealy, S. G. & Hobson, K. A. 1992. Behavioural defences against brood parasitism in sympatric host populations. *Evolution*, **46**, 334–340.
- Brooke, M. de L. & Davies, N. B. 1988. Egg mimicry by cuckoos *Cuculus canorus* in relation to discrimination by hosts. *Nature*, **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.
- Catchpole, C. K. 1974. Habitat selection and breeding success in the reed warbler (*Acrocephalus scirpaceus*). *Journal of Animal Ecology*, **43**, 363–380.
- Chance, E. 1940. *The Truth about the Cuckoo*. London: Country life.
- Davies, N. B. & Brooke, M. de L. 1988. Cuckoos versus reed warblers: adaptations and counteradaptations. *Animal Behaviour*, **36**, 262–284.
- Davies, N. B. & Brooke, M. de L. 1989a. An experimental study of co-evolution between the cuckoo, *Cuculus canorus*, and its hosts. I. Host egg discrimination. *Journal of Animal Ecology*, **58**, 207–224.
- Davies, N. B. & Brooke, M. de L. 1989b. An experimental study of co-evolution between the cuckoo, *Cuculus canorus*, and its hosts. II. Host egg markings, chick discrimination and general discussion. *Journal of Animal Ecology*, **58**, 225–236.
- Davies, N. B., Bourke, A. F. G. & Brooke, M. de L. 1989. Cuckoos and parasitic ants: interspecific brood parasitism as an evolutionary arms race. *Trends in Ecology and Evolution*, **4**, 274–278.
- Dawkins, R. & Krebs, J. R. 1979. Arms races between and within species. *Proceedings of the Royal Society of London, Series B*, **205**, 489–511.
- Edvardsen, E. 1998. Host preferences in the cuckoo *Cuculus canorus*. Masters thesis, Norges Teknisk-Naturvitenskapelige Universitet, Våren, Norway.
- Evans, D. R. & Gates, E. J. 1997. Cowbird selection of breeding areas: the role of habitat and bird species abundance. *Wilson Bulletin*, **109**, 470–480.
- Fisher, R. A. 1954. *Statistical Methods for Research Workers*. 12th edn. Edinburgh: Oliver & Boyd.
- Gates, E. J. & Evans, D. R. 1998. Cowbirds breeding in the central Appalachians: spatial and temporal patterns and habitat selection. *Ecological Applications*, **8**, 27–40.
- Gibbs, H. L., Sorenson, M. D., Marchetti, K., Brooke, M. de L., Davies, N. B. & Nakamura, H. 2000. Genetic evidence for female host-specific races of the common cuckoo. *Nature*, **407**, 183–186.
- Glück, E. 1984. Habitat selection in birds and the role of early experience. *Zeitschrift für Tierpsychologie*, **66**, 45–54.
- Grünberger, S. & Leisler, B. 1990. Angeborene und erfahrungsbedingte Komponenten der Habitatwahl der Tannenmeise (*Parus ater*). *Journal für Ornithologie*, **131**, 460–464.
- Grünberger, S. & Leisler, B. 1993a. Auswirkung der Umwelterfahrung auf die Neophobie der Tannenmeise (*Parus ater*). *Journal für Ornithologie*, **134**, 352–355.
- Grünberger, S. & Leisler, B. 1993b. Die Ausbildung von Habitatpräferenzen bei der Tannenmeise (*Parus ater*): genetische Prädisposition und Einfluss der Jugenderfahrung. *Journal für Ornithologie*, **134**, 355–358.
- Klopfer, P. H. 1963. Behavioral aspects of habitat selection: the role of early experience. *Wilson Bulletin*, **77**, 376–381.
- Krebs, J. R. & Davies, N. B. 1993. *An Introduction to Behavioural Ecology*. 3rd edn. Oxford: Blackwell Scientific.
- Lack, D. 1968. *Ecological Adaptations for Breeding in Birds*. London: Methuen.
- Latter, H. O. 1902. The egg of *Cuculus canorus*: an inquiry into the dimensions of the cuckoo's egg relation and the relation of the variations to the size of eggs of the foster-parent, with notes of coloration. *Biometrika*, **1**, 164–176.
- Lotem, A., Nakamura, H. & Zahavi, A. 1995. Rejection of cuckoo eggs in relation to host age: a possible evolutionary equilibrium. *Behavioral Ecology*, **3**, 128–132.
- Mazur, K. M., Frith, S. D. & James, P. C. 1998. Barred owl home range and habitat selection in the boreal forest of central Saskatchewan. *Auk*, **115**, 746–754.
- Moksnes, A. & Røskaft, E. 1995. Egg-morphs and host preference in the common cuckoo (*Cuculus canorus*): an analysis of cuckoo and host eggs from European museum collections. *Journal of Zoology*, **236**, 625–648.
- Moksnes, A., Røskaft, E., Braa, A. T., Korsnes, L., Lampe, H. L. & Pedersen, H. C. 1991. Behavioural responses of potential hosts towards artificial cuckoo eggs and dummies. *Behaviour*, **116**, 64–89.
- Morton, E. S. 1990. Habitat segregation by sex in the hooded warbler: experiments on proximate causation and discussion of its evolution. *American Naturalist*, **135**, 319–333.

- Newton, A.** 1893. *A Dictionary of Birds. Part 1.* London: Black.
- Olson, G. S. & van Horne, B.** 1998. Dispersal patterns of juvenile Townsend's ground squirrels in southwestern Idaho. *Canadian Journal of Zoology*, **76**, 2084–2089.
- Partridge, L.** 1974. Habitat selection in titmice. *Nature*, **247**, 573–574.
- Rensch, B.** 1924. Zur Entstehung der Eimimikry der Kuckuckseier. *Journal für Ornithologie*, **72**, 461–472.
- Rothstein, S. I.** 1990. A model system for coevolution: avian brood parasitism. *Annual Review of Ecology and Systematics*, **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.
- Soler, M., Soler, J. J., Martinez, J. G. & Møller, A. P.** 1994. Micro-evolutionary change in host response to a brood-parasite. *Behavioral Ecology and Sociobiology*, **35**, 295–301.
- Southern, H. N.** 1954. Mimicry in cuckoo's eggs. In: *Evolution in Process* (Ed. by J. Huxley, A. C. Hardy & E. D. Ford), pp. 257–270. New York: Collier Books.
- Swihart, R. K. & Slade, N. A.** 1985. Testing for independence of observations in animal movements. *Ecology*, **66**, 1176–1184.
- Taborsky, B. & Taborsky, M.** 1992. Spatial organization of the North Island brown kiwi *Apteryx australis mantelli*: sex, pairing status and territoriality. *Ibis*, **134**, 1–10.
- Taborsky, B. & Taborsky, M.** 1995. Habitat use by the brown kiwi (*Apteryx australis mantelli*) in a patchy environment. *Auk*, **112**, 680–689.
- Teuschl, Y., Taborsky, B. & Taborsky, M.** 1994. Habitat imprinting and Egg Mimicry in European cuckoos. *Journal für Ornithologie*, **135**, 137.
- Teuschl, Y., Taborsky, B. & Taborsky, M.** 1998. How do cuckoos find their hosts? The role of habitat imprinting. *Animal Behaviour*, **56**, 1425–1433.
- Thorpe, W. H.** 1939. Further experiments on preimaginal conditioning in insects. *Proceedings of the Royal Society of London, Series B*, **127**, 471–482.
- Thorpe, W. H.** 1945. The evolutionary significance of habitat selection. *Journal of Animal Ecology*, **14**, 67–70.
- Wecker, S. C.** 1963. The role of early experience in habitat selection by the prairie deer mouse, *Peromyscus maniculatus bairdi*. *Ecological Monographs*, **33**, 307–324.
- Worton, B. J.** 1987. A review of models of home range for animal movement. *Ecological Modelling*, **38**, 277–298.
- Wyllie, I.** 1981. *The Cuckoo*. London: Batsford.