HABITAT AND SPACE USE OF EUROPEAN CUCKOO FEMALES DURING THE EGG LAYING PERIOD

by

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Summary

In brood parasites, knowledge of spacing behaviour, habitat use and territoriality may reveal cues about how parasites find and use their hosts. To study the use of space and habitat of European cuckoos, *Cuculus canorus*, we radio-tagged 16 females during four consecutive reproductive seasons. We hypothesized that during the laying period cuckoo females should (1) use habitats selectively, and (2) attempt to monopolize potential egg laying areas to reduce competition for host nests. Our data are consistent with the first hypothesis: the use of pond edges compared to forest and transitional habitats was significantly greater than expected from the habitat availability in the total area and within individual female home ranges. All 26 directly observed egg layings and 27 nest visits without laying occurred at pond edges in nests of *Acrocephalus* spp. Females spent significantly more time at pond edges on egg-laying days than on non-laying days. The second hypothesis was not supported: female home ranges overlapped similarly in all three major habitat categories of the potential egg laying areas, and only little aggression was observed between females. We discuss whether female

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cuckoos may lack territorial behaviour because they are not able to defend egg laying areas economically or because defence is not necessary due to sufficient availability of suitable host nests.

Introduction

Common cuckoos (*Cuculus canorus*) are obligate brood parasites of various passerine species. Cuckoo eggs often match the host eggs in colour and pattern ('egg mimicry'; *e.g.* Jourdain, 1925; Moksnes & Røskaft, 1995), and it is generally believed that each female cuckoo lays a distinctive type of eggs that matches the egg type of its particular host species (Chance, 1940; Davies & Brooke, 1988; Moksnes & Røskaft, 1995). Furthermore specialized 'gentes' of cuckoo females parasitzing particular host species have been documented with help of molecular genetic analyses (Gibbs *et al.*, 2000). If the egg type of a cuckoo female mimics that of her host, her eggs are less likely to be detected and removed by the host (*e.g.* Davies & Brooke, 1988). Therefore cuckoo females laying mimetic eggs should specialize on a particular host species. Indeed females of a Japanese population of *C. c. telephonus* were found to be highly host specific (Marchetti *et al.*, 1998).

The question of how females recognize and find the nest of their host species is still under debate (*e.g.* Rothstein & Robinson, 1998). Four mechanisms have been proposed to allow cuckoo females to find the right hosts: host imprinting, a genetically determined preference, philopatry and habitat imprinting (for reviews of the hypotheses see Brooke & Davies, 1991; Teuschl *et al.*, 1998). As yet, evidence was found only for the habitat imprinting hypothesis (Teuschl *et al.*, 1998); in lab experiments, first-year cuckoos preferred those habitats for watching potential hosts, in which they had been hand-raised, suggesting that habitat may play a crucial role in the host finding process. At present, very little information is available on the importance of habitat for the spacing and laying behaviour of cuckoo females in the wild (Vogl *et al.*, 2002).

Searching and observing nests suitable to be parasitized is a very time consuming process for cuckoo females (Wyllie, 1981; Davies & Brooke, 1988; Øien *et al.*, 1996). If the habitat is used by females as a cue telling them where to search for appropriate host species and nests (as was proposed by Teuschl *et al.*, 1998), we expect (a) that females show a preference for particular laying habitats, and (b) that this preference is more pronounced around egg laying. As yet, it has not been investigated which habitats females use preferentially during their breeding season as compared to habitat availability, and whether preferences vary with the stage of the laying period.

Once a female found a suitable host nest for egg laying, she may face competition with other females for this nest (Chance, 1940; Wyllie, 1981). Evidence for exclusive territory defence of cuckoo females is equivocal. While some studies report the existence of breeding territories (Dröscher, 1988), others found overlapping areas and/or multiple parasitism of different females in the same nest (Molnar, 1944; Davies & Brooke, 1988; Nakamura & Miyazawa, 1997). Aggression between females has been observed at various levels: calling behaviour (Nakamura & Miyazawa, 1997), chases by resident females to restrain the access of other females to nests or territories (Riddiford, 1986), and occasional fights between females (see Wyllie, 1981). If more than one female parasitizes the same host nest only one cuckoo chick can survive. Additionally, other cuckoo females may depredate host nests containing already an egg by a resident female, or they may even selectively remove another cuckoo egg detected in a clutch before laying their own egg (Davies & Brooke, 1988). Hence we expect females to attempt to monopolize certain areas containing suitable nests (see Dröscher, 1988). Egg laying areas of individual females should overlap only little and females should defend nests or egg laying areas.

We followed radio-tagged females of a cuckoo population parasitizing four species of the genus *Acrocephalus*. These hosts breed either in reed or in herb vegetation or in a mixture of both. Our study population was especially suited to investigate habitat preferences as the areas used for egg laying and for feeding by individual cuckoos were contiguous or nearly contiguous. Hence commuting costs between feeding and breeding areas should be low, and cuckoo females should be able to switch between habitats frequently, according to their actual needs.

Methods

Study species and area

We studied the European subspecies of the cuckoo *C. c. canorus*, which breeds from end of April, immediately after return from Africa, until early or mid July (Wyllie, 1981; own obs.). Eggs are laid usually at intervals of two days (Chance, 1940; Wyllie, 1981; own obs.).

The study area was located in a commercially used carp pond area in Southern Moravia, Czech Republic, with nearby forests consisting mainly of mixed-age oak and pine stands.

Narrow strips of different vegetation types lined the pond edges. We distinguish between two gross habitat categories, the ‘potential laying area’, where in principal egg laying by cuckoos was possible, and the remaining ‘unsuitable area’, such as built-up area, water surface and agricultural land, which was crossed by cuckoos but not used for feeding or nest-searching.

In the potential laying area we distinguished between three habitats, ‘pond edges’, ‘forests’ and ‘transitional zone’. Each of these habitats consisted of different ‘vegetation types’, which are defined as parts of a habitat with typical and homogeneous vegetation (cf. Taborsky & Taborsky, 1995).

(a) Vegetation at pond edges included reed vegetation consisting of the vegetation types ‘reed’, ‘reed mixed’ (including herbs up to 20%) and ‘reed mace’. Potential cuckoo hosts in these vegetation types were great reed warblers (*Acrocephalus arundinaceus*) and reed warblers (*A. scirpaceus*). Further, there was herb vegetation consisting of the vegetation types ‘herbs’, ‘nettles’, and ‘herbs mixed’ (with usually >50% *Solidago canadiensis* and reed up to 20%). Here, marsh warblers (*A. palustris*), sedge warblers (*A. schoenebaenus*), and reed buntings (*Emberiza schoeniclus*) were potential cuckoo hosts. All vegetation types were partly interspersed with bush rows and groups of trees (*Salix* sp. and *Acer negundo*). Robins (*Erithacus rubecula*), wrens (*Troglodytes troglodytes*), and garden warblers (*Sylvia borin*) were potential cuckoo hosts in these bushes and trees, but had very low breeding densities in our study area (A. Moksnes, pers. comm.).

(b) Forests surrounding the ponds were managed for timber production and consisted of the vegetation types ‘uniform oaks’ (*Quercus* sp.), ‘oaks mixed’ (including oaks of different ages and other tree species), ‘young oaks’ (up to a height of *ca* 3 m), ‘pines’ (*Pinus sylvatica*), ‘young pines’ (up to a height of *ca* 3 m), ‘robinias’ (*Robinia pseudacacia*) and ‘alders’ (*Alnus glutinosa*). Potential hosts in this habitat were robins (*E. rubecula*) and tree pipits (*Anthus trivialis*).

(c) The transitional zone with a variety of herbs, bushes and trees of up to 5 m height, consisted of the vegetation types ‘forest edge’ (longitudinal strips bordering forest) and ‘clearings’ (patches surrounded by forest). Potential hosts in this habitat were nightingales (*Luscinia megarhynchus*) and wrens (*Troglodytes troglodytes*).

Other potential cuckoo hosts in the study area, including wagtails (*Motacilla alba*), black redstarts (*Phoenicurus ochruros*) and yellowhammers (*Emberiza citrinella*), occurred only at very low densities (A. Moksnes pers. comm., own obs.).

Mapping of vegetation types

The distribution of vegetation types within forests and the transitional zone was derived from a forest management map and recent aerial photographs. At the pond edges, vegetation types are typically distributed in long, narrow strips or in small patches. In this habitat we mapped the vegetation types with help of transects laid perpendicular to the shoreline of ponds and channels, in steps of 10 m distance from each other. 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 transects and the proportions and heights of different plant species.

Catching and handling of birds

We caught cuckoos with mist nets between early May and early June 1995-1998, mostly by luring them with playbacks of alternating male and female cuckoo calls. All catching was done at the pond edges. We took the body weight and the length of bill, tarsus, tail and wing of each bird. Wing tags made of coloured sheets of plastic were attached to the prepatagial part of the wing. We glued miniature radio transmitters (type SS-2, Biotrack, Dorset, UK; 2.5 g including battery, *ca* 2.5% of female body mass) with cyanoacrylate to the upper side of the central tail feather, with the antenna tied alongside the feather. The batteries of transmitters lasted about 60 days and the signal detection range was 0.75-2 km. The transmitters did not appear to affect the reproductive activities of the cuckoos. In some cases we observed male courtship and females searching for nests already the next day and egg laying within four days after handling. We radio-tagged 16 females (one of them in 2 successive years) and 18 males. Home range and spacing data presented in this paper include females only, while behavioural data are included of both sexes.

Radio-tracking

Five observers collected data between May and early July 1995-1998. We followed the birds mainly by bicycle and on foot. Over larger distances we used a motorcycle or a car. The birds were located by 'homing in' to the individual (Kenward, 2001) and the locations noted on maps of 1:10000 scale, together with time of day and behaviour. Triangulation from different positions was used to estimate the birds' location where a close approach to the animal was impossible (depending on the method of tracking we estimated the location accuracy to vary between 10 and 50 m). Most radio-tracking data were collected during continuous focal animal recordings, which served to achieve data on social behaviour of cuckoos and to observe egg layings. During these recordings, each detectable move of a focal bird was noted and locations were mapped whenever a bird had moved more than 20 m from its previous location. Locations and behavioural activities were mainly recorded between 05:30 h and 08:30 h and 14:00 h and 21:00 h. Courtship and other interactions were observed best in the early morning and late evening, and most egg layings occurred between 14:00 and 19:00 (see also Wyllie, 1981; Moksnes & Røskaft, 1987; Moksnes *et al.*, 1991; Nakamura & Miyazawa, 1997).

Behavioural observations

Behavioural data were collected within focal animal recordings, where one observer followed a single bird continuously for at least 30 min (up to 8 hours). Together with the location of a focal bird we noted (i) the time and duration of its calls and of all other cuckoo males and females heard within 250 m of the focal bird, and (ii) all social interactions of the focal bird with other cuckoos. Here we present behavioural data from focal recordings, during which at least one cuckoo was heard, seen or tracked within 250 m of the focal bird (535 h 32 min focal recordings of females, 147 h 41 min focal recordings of males). We chose 250 m as a threshold distance, as at this distance we were able to hear cuckoo calls of both sexes unambiguously. We assumed that this should also be the least distance at which cuckoos hear each other, and hence should be able to react to conspecifics. We report frequencies of two types social interactions: 'Follow-up flights', where two cuckoos fly closely one after the other, and 'response calls', where a cuckoo call is followed by a second cuckoo's call within 60 seconds when both birds are 50 m or less apart from each other.

Data analyses

Range sizes were calculated from digitized location information using an adaptive kernel estimator (Worton, 1987, 1995) with help of the software package 'HOME' developed by H. Winkler (see Taborsky & Taborsky, 1992). This method is based on a bivariate probability density function. As estimate for cuckoos home ranges we used the area integrating 90% of the calculated density distribution. As we aimed to record all detectable moves and locations of the cuckoos during focal recordings for behavioural analyses, a large proportion of locations was only separated by extremely short time intervals and distances. Moreover, as the cuckoos often stayed for extended periods in a small region of their home range switching their position at a fast rate (especially during the early morning and late evening hours when most social interactions took place), the location data were highly clumped in space and time. De Solla *et al.* (1999) showed that excluding too many locations for the sake of achieving independence of data may reduce the biological relevance of the home range estimates. However, due to our peculiar data structure we felt that a selection of representative points from the data clumps was nevertheless necessary to reduce the bias of the density distribution we calculated from the locations to estimate home ranges. As an objective measure of data selection we calculated the 'time to independence' (TTI) intervals for each individual cuckoo (Swihart & Slade, 1985), which were between $1'30''$ and $3'45''$ h in our cuckoos. We used the locations recorded at intervals larger than the TTI for home range estimates.

In total, 2180 data points were obtained, of which 323 fixes were classified as independent ($\bar{x} \pm \text{SD} = 32.3 \pm 14.23$ fixes per female). We calculated home range sizes for sample sizes of 10 or more independent locations (Table 1). A similar study on brown kiwis, *Apteryx australis*, showed that estimates using this sample size gave reliable home range sizes (cf. Appendix 1 in Taborsky & Taborsky, 1992). We excluded 7 females entirely from the analyses. The signals of the transmitters of these birds were lost briefly after catching ($\leqslant 6$ days of radio-tracking) due to transmitter failure or because the birds may still have been on migration. We excluded these birds, as for a representative home range estimate the total time period a bird is tracked must be sufficiently long (De Solla *et al.*, 1999). Moreover, we did not obtain sufficient independent locations of these females. For two of the nine females we did not detect their feeding ranges. Therefore *total* home range sizes have been calculated from seven females only. Of the female tracked in two years, we used only the data from the first year of capture (1995) for statistical analyses except for the calculation of concurrent home range overlaps.

Areas of the transitional zone were always very small and adjacent to or within the forest. If birds were not seen or heard directly it was often impossible to determine whether they were sitting in the forest or at a forest edge or clearing, even when they were tracked from a close distance. Therefore, we combined forest and transitional zone into one habitat category called 'F + T habitat' for the analysis of habitat preferences of cuckoo females. Location counts in different habitat categories follow a multinomial distribution (Manly *et al.*, 1993). As we analyse two habitat categories only, we calculated binomial tests for each bird to compare location counts in the habitat categories within each home range (habitat use) with expectations derived from the respective habitat availability. Results for individual females were combined for an overall test of significance following the procedure proposed by Fisher (1954).

For estimating habitat use we included only the first locations recorded in each of four time periods that were distributed equally over the day (06:30-07:30, 11:30-12:30, 14:30-15:30, and 18:30-19:30) to ensure that data points were spatially and temporally independent. Independent data are required when habitat use is estimated directly from location data

TABLE 1. *Number of independent locations, number of days tracked and numbers of days from catching to last day of tracking (in brackets), individual home range sizes of female cuckoos and habitats in ha*

Female	# indep. locations	Days tracked	Home range size	Potential egg laying area	Forest	Transitional zone	Pond edges
14/96	20	8 (8)	32.7	24.9	24.0	0.1	0.8
5/95	26	9 (12)	34.2	27.3	17.3	3.7	6.3
11/96	33	17 (17)	47.5	25.8	23.0	0.1	2.7
3/95	44	28 (30)	60.8	24.1	18.0	1.3	4.8
5/97	50	34 (38)	107.1	69.0	63.5	0.9	4.6
2/97	57	33 (51)	123.2	82.6	70.2	2.5	9.9
F/95$^+$	30	14 (25)	314.6	179.0	156.5	10.2	12.3
median	**33**	**17 (25)**	**60.8**	**27.3**	**24.0**	**1.3**	**4.8**
quartiles	28	11.5 (14.5)	40.88	25.3	20.5	0.5	3.6
	47	30.5 (34)	115.1	75.8	66.9	3.1	8.1
F/96$^+$	22	11 (16)	121.1	66.8	60.5	0.6	5.7
10/95*	11	8 (10)	*13.4*	*7.5*	*2.3*	*0.2*	5.0
3/98*	30	19 (27)	*39.3*	*17.5*	*13.0*	*0.1*	4.3

$^+$ F/95, F/96, p. same female tracked in two years; only the range from 1995 was included in the calculation of the medians.

* We could not estimate the total home ranges for females 10/95 and 3/98 because due to weak transmitters we did not detect their feeding ranges (the area of forest and transitional zone used by these females in direct vicinity of their breeding sites is given in italics).

(Aebischer *et al.*, 1993; Manly *et al.*, 1993). These data points were also used to compare habitat use between laying and non-laying days of each female. Habitat availability was estimated from habitat proportions of (1) the entire study area, and (2) individual females' home ranges. The use of the two habitats are entirely intercorrelated: a preferential use of one habitat must necessarily lead to a less intense use of the other habitat (*cf.* Aebischer *et al.*, 1993). Hence for any deviation of habitat use from expectation, we cannot distinguish whether this is due to a preference for one habitat or to an aversion against the other habitat.

We used non-parametric statistics throughout, as distributions differed significantly from normality or data were too sparse to test reliably for deviations from normality. For descriptive statistics, medians and quartiles (q_1, q_3) are given.

Results

Home range size and habitat composition

Female home ranges encompassed on average 60.8 ha (= median) but varied greatly in size (Table 1). They contained on average 27.3 ha of potential laying area (Table 1), while 36.7 ha ($q_1 = 14.8$, $q_3 = 39.3$) were classified as being unsuitable for laying. There was no notable difference between the habitat distribution in the total study area and within home ranges (forest: 86.1% *vs* 87.4% (= median), transitional zone: 8.3% *vs* 3.0%, pond edges: 5.% *vs* 10.2%).

The largest proportions of pond edges consisted of herb vegetation (herbs mixed, herbs and nettles) in five female home ranges, and of reed vegetation (reed, reed mixed and reed mace) in four home ranges (Table 2). Home ranges were structured in two regions, an area were most reproductive activities were observed but foraging occurred rarely (further termed 'breeding range'), and an area which was used for feeding, roosting and other activities (termed 'feeding range'). Three female home ranges were contiguous, while in four home ranges the breeding and feeding range were 500 m apart (= the median closest distance between any two telemetry fixes between the two regions, range = 380-600 m; median for all 7 females = 380 m). The feeding ranges of two females were not found.

We correlated the proportions of habitats included in a home range with total home range size. A negative relationship would mean that a similar absolute amount of a habitat is present in the home ranges. A positive correlation would mean that the amount of a habitat increases over-proportionally with home range size. We found no relationship between any of the habitats and home range size (Spearman rank correlations, $N = 7$ females, forest: $r_s = -0.21$, transitional zone: $r_s = 0.29$, pond edge: $r_s = 0$, all $p > 0.1$).

Are specific habitats in the 'potential laying area' preferred for reproduction?

The location counts in the two habitats differed significantly from the proportions of habitat present in the home ranges (Table 3; test to combine probabilities after Fisher 1954, $N = 7$, $\chi^2_{[14]} = 90.9$, $p < 0.001$) and in the entire study area ($N = 7$, $\chi^2_{[14]} = 96.7$, $p < 0.001$), with pond edges being used more often than expected and, correspondingly, the F+T habitat used less often than expected (Fig. 1).

TABLE 2. *Habitat composition (vegetation types in %) of the potential laying area*

	3/95	5/95	11/96	14/96	2/97	5/97	F/95^{+}	F/96^{+}	10/95*	3/98*
Transitional zone:										
Forest edges	0.7	1.9	**1.5**	**1.6**	1.0	**1.3**	1.7	**1.0**	***3.2***	***0.6***
Clearings	**4.8**	**11.8**	0.0	0.0	**2.1**	0.0	**4.0**	0.0	*0.0*	*0.0*
Forest:										
Oaks uniform	**41.8**	**30.6**	**74.8**	**78.2**	24.0	**62.3**	**46.3**	**51.4**	*0.0*	*19.2*
Oaks mixed	0.0	12.8	1.6	2.2	**44.5**	11.6	12.9	19.5	*5.5*	***55.5***
Young oaks	17.2	0.0	1.0	1.0	2.1	1.1	2.0	5.2	*0.0*	*0.0*
Pines	12.4	19.9	0.0	7.0	7.0	8.4	11.5	7.5	*0.0*	*0.0*
Young pines	0.0	0.0	0.0	0.0	3.4	3.1	2.6	0.0	*0.0*	*0.0*
Robinias	3.2	0.0	0.0	0.0	3.9	0.7	10.7	4.0	***24.8***	*0.0*
Alders	0.0	0.0	10.8	6.8	0.0	4.9	1.5	2.9	*0.0*	*0.0*
Pond edges:										
Bush rows	4.1	2.2	3.4	0.7	1.7	1.6	1.7	2.6	0.0	3.4
Reed	0.5	5.7	1.6	**1.6**	3.2	0.6	1.8	1.2	**40.7**	3.2
Reed mixed	0.4	5.1	0.1	0.1	2.5	0.5	0.1	0.2	0.0	1.1
Reed mace	0.1	0.3	0.2	0.0	0.1	0.0	0.1	0.3	0.0	1.6
Herbs mixed	**9.7**	**8.1**	**4.2**	0.7	**3.3**	**3.4**	**2.2**	**2.8**	25.8	**11.2**
Herbs	4.0	1.3	0.7	0.1	0.7	0.3	0.6	1.0	0.0	2.5
Nettles	1.1	0.3	0.2	0.1	0.4	0.2	0.3	0.4	0.0	1.8

Rows: vegetation types in the three habitats. Columns: female cuckoos. Each column sums up to 100%. Bold numbers indicate the prevailing vegetation type of each female within each habitat.

$^{+}$ F/95, F/96: same female tracked in two years.

* *cf.* Table 1.

At pond edges, a higher proportion of independent locations was recorded on laying days than on non-laying days (Wilcoxon matched-pairs signed-ranks test, $N = 6$ females, $T = 0$, $p < 0.05$, Fig. 2a) and on laying days, females also spent more time there ($N = 7$ females, $T = 0$, $p < 0.02$; Wilcoxon test). The average proportion of time females spent at pond edges three hours before they laid an egg was significantly higher than for the same period and time of day on the preceding or following non-laying day (Wilcoxon test, $N = 7$ females, $T = 0$, $z = 2.37$, $p < 0.02$, Fig. 2b). Furthermore, all observed 26 egg layings and 27 nest visits without laying by seven females occurred in the pond edge habitat.

TABLE 3. *Comparison of habitat use calculated from spatially and temporally independent locations (see 'Methods') vs habitat availability (a) in individual home ranges and (b) in the entire study area*

Female	Locations in F + T	Locations at pond edges	Proportion F + T	(a) Home range	(b) Study area
14/96	9	5	96.8	<0.001	<0.001
5/95	5	7	76.9	0.018	<0.001
11/96	13	17	89.5	<0.001	<0.001
3/95	9	39	80.1	<0.001	<0.001
5/97	35	30	93.3	<0.001	<0.001
2/97	33	26	88.0	<0.001	<0.001
F/95	8	11	93.12	<0.001	<0.001

Proportion of forest F and transitional zone T combined is 94.3%. p-values of binomial tests are given; for a test of all birds combined see 'Results'.

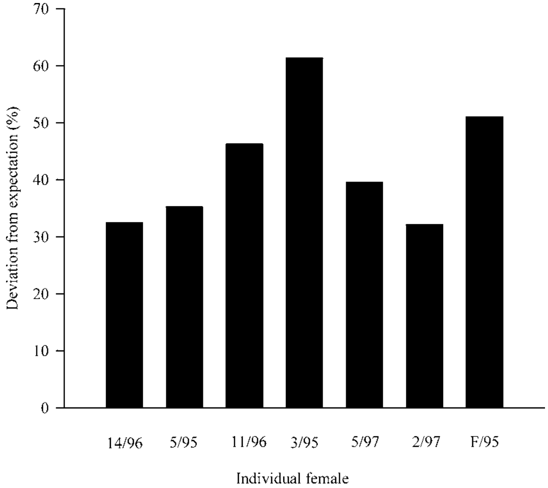

Fig. 1. Deviation of use of pond edges from expectation. Correspondingly, the use of forest and transitional zone combined deviates negatively to the same extent.

Do females defend their egg-laying areas against other females?

The home ranges of five of the seven radio-tagged females overlapped with at least one other female. The median overlap between any two of these home ranges was 20.4% ($q_1 = 8.8\%$, $q_3 = 33.5\%$). Similar overlaps were found within each habitat (medians: 18.7% for forests, 20.2% for the transitional

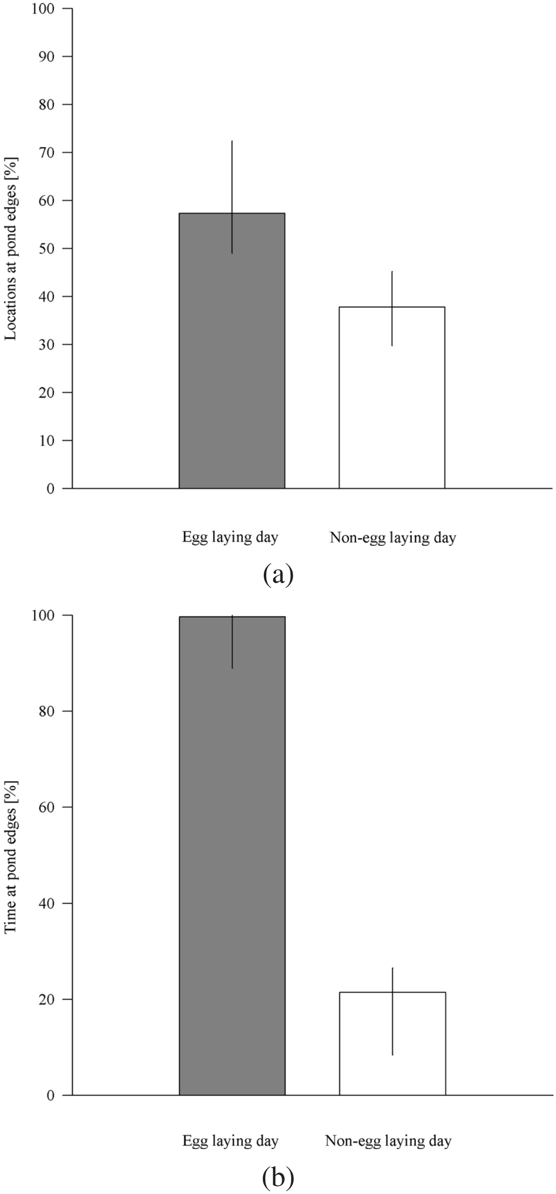

Fig. 2. (a) Average proportion of independent locations of females in the ‘pond edge’ habitat on laying days and on non-laying days (medians ± quartiles). (b) Average proportion of time the females spent at pond edges three hours before egg laying on laying days and at the corresponding time on non-laying days.

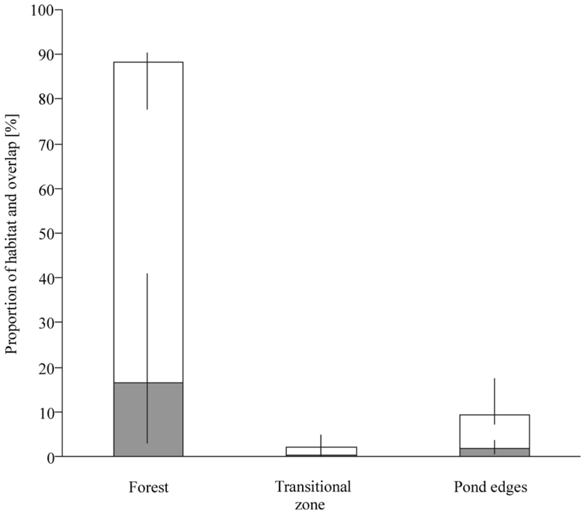

Fig. 3. Habitat proportions (medians ± quartiles) of female home ranges (total bar), and average proportions of overlap in relation to the distribution of habitats within the home ranges (grey section of bar; $N = 5$ females; the overlap with the recaptured female C95/96 was calculated for the areas occupied in 1995 and 1996 separately).

zone, 20.3% for pond edges; Fig. 3), but the sample size was too small to test for differences in overlap between habitats.

Female-female aggression was nearly absent. Fights were never observed between any two cuckoos. Other interactions within the female sex, which may potentially involve aggression were (i) follow-up flights, *i.e.* one female flies closely behind another female, and (ii) response calls between females. During the focal observations (see 'Methods'), the focal female was involved 3 times in a female-female follow-up flight (as compared to 6 male-male and 45 male-female pursuits with either a focal male or female involved). A female answered another female call in only 3 cases. In comparison, a male answered another male call in 33 cases (these frequencies include only those cases where no bird of the opposite sex was calling as well).

Discussion

Home range composition and use

Cuckoo females used their home ranges differentially with regard to the two main functions we were investigating. Feeding occurred rarely at pond edges, while reproductive activities were observed predominantly in this habitat. All 53 directly observed nest visits of cuckoos with or without laying, all three observed copulations, and the majority of close interactions between males and females (own unpubl. data) occurred at the pond edges. There, host density was substantially higher than in forest and in the transitional zone (Moksnes pers. comm.). Separate feeding and breeding areas were also observed in other cuckoo populations (Wyllie, 1981; Dröscher, 1988 for *C. c. canorus*; Nakamura & Miyazawa, 1997 for *C. c. telephonus*) and in parasitic cowbirds (Rothstein *et al.*, 1984; Evans & Gates, 1997; Gates & Evans, 1998).

In *C. c. telephonus*, females travelled several kilometres between breeding and feeding areas. Here commuting costs affected the time females spent in a habitat and the frequency of switching between them (Nakamura & Miyazawa, 1997). Due to the close proximity of forests providing good feeding grounds and pond edges with a high host density, travel distances between feeding and breeding ranges in our study area were short. It is unlikely that commuting costs affected the times females spent in different habitats to a larger degree.

The peculiar structure of laying habitat in our study area may also explain why the areas used for egg laying were much smaller in our population than in the Japanese population of cuckoo females parasitizing great reed warblers (our study: 4.8 ha; Nakamura & Miyazawam, 1997: 51.2 ha). The pond edge habitat consisted of long and narrow strips surrounding fish ponds, while in Japan female breeding ranges included wide reed beds and other large-scale habitats.

In our study area home range sizes of female cuckoos varied widely between 33 and 217 ha. A similar or even larger variation of range sizes was found also in other populations of brood parasites (12 to 58 ha, Gates & Evans, 1998; 31.1 to 403.2 ha of feeding area plus breeding area, and 101 to 677 ha of total home range size including travel area, Nakamura & Miyazawa, 1997). In our population the extent of variation is mainly caused by variation in the size of the large feeding ranges (19.3 to 113.9 ha), which consisted of a patchwork of oak and pine stands. Depending on the distribution of vegetation types within the forested parts of their home ranges, females had to travel different distances between suitable feeding locations.

Areas with pond edges made up on average 10.5% of home ranges. They were less variable in size than other habitats (ratio of interquartile range over median: 1.9 for forest, 2.0 for the transitional zone, 0.9 for pond edges). The small variation in the sizes of pond edge areas within home ranges may suggest that cuckoo females have a minimum need for suitable egg laying habitat that is similar between individuals. In this case a negative correlation would be expected between the area of this habitat and overall range size (see Taborsky & Taborsky, 1995). However, home range size did not correlate with the proportion of pond edges nor with any other habitat. One reason for a lacking relationship may be an inhomogeneous distribution and density of potential host nests. Of the three host species used by radio-tagged females, reed warblers have smaller territories and occur more densely than marsh and sedge warblers (Glutz & Bauer, 1991). Due to small sample size we were unable to test for an effect of host species on the sizes of laying areas.

Are specific habitats preferred for reproductive activities?

Egg laying was exclusively observed in the pond edge habitat (see Nakamura & Miyazawa, 1997 for a similar observation). Habitat use deviated significantly from expectation, with pond edges being more preferred than forests and transitional zone combined. Pond edges were used more intensively on egg-laying days than on non-egg laying days. These data are consistent with the hypothesis that a selective use of habitats may help females to find suitable nests (Teuschl *et al.*, 1998). Our results provide the first quantitative comparison of habitat availability and use in cuckoos. A consistent preference for laying habitats was also found on the level of microhabitat (reed *vs* herb vegetation, Vogl *et al.*, 2002), which further corroborates the importance of habitat for nest finding in cuckoos. A preference of certain habitats for breeding purposes, which are not necessarily preferred for other activities such as foraging or roosting has been shown in other bird species as well (*e.g.* Gates & Evans, 1998 for cowbirds; Taborsky & Taborsky, 1995 for kiwis, *Apteryx australis*). Alternatively, the observed habitat preference could be a by-product of some other factor leading to extended stays of cuckoo females at pond edges. Cuckoo females may be attracted by certain visual or acoustical host cues, as it was suggested for cowbirds (Clotfelter, 1998; Banks & Martin, 2001; Robinson & Robinson, 2001). So far, experimental results have failed to demonstrate that cuckoos pay attention to host cues (Brooke & Davies, 1991). Nevertheless, we think that host cues may still be involved in nest finding, but this should occur at a later stage of nest finding process, which can be imagined to be organized hierarchically (see Teuschl *et al.*, 1998). While habitat selection may aid in finding areas containing suitable nests, host cues or nest site cues (Moksnes & Røskaft, 1995) may be used for the fine tuning of the actual nest choice within this habitat.

Do females defend their egg-laying areas against other females?

As suggested by earlier studies (*e.g.* Chance, 1940; Wyllie, 1981; Dröscher, 1991), we expected that females will defend their laying areas against competing cuckoos. However, our data refute the hypothesis of female territoriality, both at the levels of space use and of observed behaviours. On average, 20% and up to 86% of the pond edge habitat in a female's home range was used by a neighbouring cuckoo female as well. While these figures compare only the home range overlap between two neighbouring females, a female's range may overlap with the ranges of several female neighbours (up to three among our radio-tracked cuckoos). As we were able to catch only a small proportion of females in our study area, the full extent of this multiple overlap could not be determined quantitatively. Different cuckoo egg types were found in host nests within individual female home ranges and sometimes even in single host nests (Moksnes, pers. comm.). Also, in two cases a cuckoo egg was replaced by a different egg type (Moksnes, pers. comm. and own obs.). The degree of overlap was similar between pond edges (20%) and forest (18.7%), which is in constrast to our expectation that the laying area should be more strongly contested than feeding grounds. Observations of direct aggression or territorial calls between females were nearly absent in 535 hours of focal female observations in four different breeding seasons.

Also home ranges of *C. canorus telephonus* overlap to a substantial degree (Nakamura & Miyazawa, 1997). In this population the large laying areas of on average 51 ha may be not economically defendable. This argument does not apply, however, to the small laying areas of our population (4.8 ha on average). There are two potential explanations why females of our population did not defend laying areas. (i) Despite their small size, laying areas are not defendable, because either the density of conspecifics is too high, or the specialized diet of cuckoos (mainly large caterpillars) forces them to feed outside their breeding range, thereby constraining their ability to defend the laying area. Nevertheless, some parasitic cowbirds are able to be truly territorial in their breeding areas (Dufty, 1982; Darley, 1982; Gates & Evans, 1998), despite the fact that they commute several kilometres between feeding and breeding areas (Gates & Evans, 1998). (ii) Territory defence is not necessary, as sufficient suitable host nests are available for more than one female. In our study area on average 2.2 (range 1-5) nests suitable for parasitism (*i.e.* in the 1 to 3 egg-stage) were present within a female's laying area on each day on which an egg laying was observed (Vogl *et al.*, 2002). Over 70% of these nests matched the females' preferences for either vegetation type or host species.

In conclusion, our data show that there is a clear habitat preference of cuckoo females when it comes to reproduction. Apparently they rely on one specific habitat for egg laying, and there is evidence that females even specialize on different vegetation types within the pond edge habitat (Vogl *et al.*, 2002). Nevertheless, females do not defend these highly valuable areas, which may be due to a constraint on economic defendability, a lack of necessity due to a high availability of nests, or both.

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