RESEARCH ARTICLE

Bimodal habitat use in brood parasitic Common Cuckoos (*Cuculus canorus*) revealed by GPS telemetry

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ABSTRACT

Obligate brood parasitic birds have evolved a rare avian strategy for reproduction by laying eggs in the nests of other species. In doing so, their breeding ranges, but not necessarily their foraging habitats, have become intimately related to the nesting territories of their hosts. We studied home range sizes and distribution patterns in Common Cuckoos (*Cuculus canorus*) on their breeding grounds in central Hungary, where cuckoos parasitize only Great Reed Warblers (*Acrocephalus arundinaceus*) in channel-side reed-beds at a high frequency (>50%). The geographic coordinates of tagged cuckoos were monitored by high-precision, remotely downloadable non-Platform Terminal Transmitter global positioning system (GPS) loggers, attached to 9 females and 6 males. Our results revealed bimodal use of habitat patches: (1) the home ranges of male and female cuckoos were packed densely along the channels where the hosts breed, and their distribution maps had high overlaps between sexes; (2) ~71% of cuckoos also visited nearby woodland patches, presumably for foraging, where the host species was not present. The size of cuckoo home ranges varied to an unusually great extent: 0.3–185 km^2 as calculated by the minimum convex polygon method (85%), or 1–17 km^2 when calculated by the more suitable kernel density estimation (KDE) method (Utilization Distribution 85%) for patchy habitats. Male and female cuckoos had similar home range sizes as estimated by the KDE method, consisting of 1–4 areas within the 2 habitat types of channel reed-beds and woodlands. No preference was revealed for night roosting locations between the 2 habitats or sexes. Female cuckoos were more likely to use reed-beds in the afternoons, when females parasitize host nests. Remote downloadable GPS methods offer an effective way of tracking cuckoos across large areas, but the estimation of home range sizes requires caution due to this species' patchy and disconnected habitat use.

Keywords: brood parasite, *Cuculus canorus*, GPS, home range, space use, telemetry

Uso de hábitat bimodal en el parásito de nidada *Cuculus canorus* revelado por telemetría GPS

RESUMEN

Las aves que obligatoriamente son parásitas de nidada han evolucionado una rara estrategia reproductiva mediante la puesta de huevos en el nido de otras especies. Al hacer esto, sus rangos reproductivos, pero no necesariamente sus hábitats de forrajeo, han terminado íntimamente relacionados a los territorios de anidación de sus hospederos. Estudiamos los tamaños de los rangos de hogar y los patrones de distribución de *Cuculus canorus* en sus sitios reproductivos en el centro de Hungría, donde *C. canorus* solo parasita a *Acrocephalus arundinaceus* en los cauces con caña a la vera de los canales a una elevada frecuencia (más de 50%). Se monitorearon las coordenadas geográficas de los individuos marcados de *C. canorus* mediante registradores GPS de alta precisión y de descarga remota, sujetados a 9 hembras y 6 machos. Nuestros resultados revelaron un uso bimodal de los parches de hábitat. (1) Los rangos de hogar de machos y hembras se amontonaron densamente a lo largo de los canales donde se reprodujo el hospedero, y sus mapas de distribución tuvieron una alta superposición entre sexos. (2) Cerca del 71% de los individuos de *C. canorus* también visitaron los parques de bosque vecinos, presumiblemente para forrajear, donde la especie hospedera no estuvo presente. El tamaño de los rangos de hogar de *C. canorus* varió de un modo inusualmente grande: 0.3–185 km^2, calculado con el método del polígono convexo mínimo (85%), o 1–17 km^2, calculado más adecuadamente mediante el método de estimación de densidad de kernel (EDK) (UD 85%) para hábitats en parche. Los machos y las hembras de *C. canorus* tuvieron tamaños de rango de hogar similares cuando fueron estimados con el método de EDK, comprendidos por 1–4 áreas al interior de los dos tipos de hábitat, canales con cauces con caña y bosque. No se identificó ninguna preferencia para los lugares de descanso nocturno entre los dos hábitats o sexos. Las hembras presentaron mayor probabilidad de usar los cauces

con caña en las tardes, cuando las hembras parasitaron los nidos hospederos. Los métodos de descarga remota con GPS ofrecen un modo efectivo de seguir a los individuos de *C. canorus* a través de grandes áreas, pero las estimaciones de los tamaños de rango de hogar deben tomarse con precaución debido al uso de hábitat en parche y desconectado de esta especie.

Palabras clave: Cuculus canorus, GPS, parásito de nidada, rango de hogar, telemetría, uso del espacio

INTRODUCTION

In obligate avian brood parasitism, parasitic eggs are incubated and offspring are attended by a different host species (Davies 2000, Soler 2017). As parasitic birds do not build a nest and are not restricted in space to its vicinity, they may spend more time on foraging widely and searching for available host nests in diverse locations; alternatively, they may use and defend host-rich nesting habitats from other brood parasites and engage in complex social interactions (Rothstein et al. 1984).

Avian brood parasites lay eggs in many host nests. For example, the Common Cuckoo (*Cuculus canorus*) lays about 10–20 eggs annually (Wyllie 1981); typically each is deposited into a different nest of predominantly the same host species (Moskát et al. 2009). Other parasitic bird species, including the Great Spotted Cuckoo (*Clamator glandarius*), also lay many eggs per season, but may often lay multiple eggs in the same nest of their preferred host species (Martínez et al. 1998). Brood parasites specializing on one or few host species, are expected to use laying areas containing several territories of their hosts, so the brood parasites' home ranges should be larger than a single territory of their hosts. Home ranges of brood parasites are therefore expected to be related to the distribution of critical resources required for reproduction (the location, density and timing of host nesting attempts: Moskat et al. 2006), for foraging (especially for specialists, such as many cuckoo species feeding on hairy caterpillars: Löhr 1979, Wyllie 1981), and other potential habitat uses relevant for other functions (e.g., mating areas and roosting sites: Nakamura and Miyazawa 1997).

Tracking the home ranges of parasitic birds, in the absence of a focal nest or exclusively defended all-purpose territory, may represent a technical challenge, but both classical very high frequency (VHF) and modern geographic information system (i.e. global positioning system [GPS]) telemetry techniques are potential tools for studying space use and home range size in avian brood parasites (Honza et al. 2002, Williams et al. 2016). Indeed, VHF telemetry has already been successfully applied to study the home ranges of obligate parasitic Shiny Cowbirds (*Molothrus bonariensis*; Scardamaglia and Reboreda 2014, de la Colina et al. 2016), Brown-Headed Cowbirds (*M. ater*; Rothstein et al. 1984, Hahn et al. 1999, Goguen and Mathews 2001, Louder et al. 2015), and Common Cuckoos (e.g., Honza et al. 2002, Vogl et al. 2004). New GPS methods allow for the automatic collection of geographic coordinates of tagged birds during the entire day simultaneously for several bird individuals, and precisely at the points visited by the birds. For example, studies of Common Cuckoos tagged with VHF telemetry typically focused on looking for one individual at a time in its core habitat-use area, typically during a short period of the day, and had difficulty following it when it took flight (Nakamura and Miyazawa 1997).

In contrast, GPS telemetry has the potential to collect large sets of geographic coordinates with high precision on the positions of tagged birds almost continuously. However, to date few published data are available from the application of miniature GPS telemetry regarding home range sizes of brood parasitic birds during the breeding season. In recent years, the size and weight of GPS telemetry tags have become similar to platform terminal transmitter (PTT) telemetry tags, which are applied frequently for migration studies of Common Cuckoos (e.g., Willemoes et al. 2014, 2015, Hewson et al. 2016, Vega et al. 2016). There was also a successful trial that used the Argos satellite GPS method for home range estimation of Common Cuckoos throughout their annual cycle (Williams et al. 2016). However, the non-PTT method seems to be more promising for home range estimation of birds in the breeding season than the PTT GPS method, given its higher accuracy, cheaper price, and the ability to collect large numbers of fixes per day and per season (Bridge et al. 2011, Bán et al. 2018).

Acrocephalus species are frequent hosts of Common Cuckoos in Europe (Leisler and Schulze-Hagen 2011), where the largest reed warbler species, the Great Reed Warbler (*A. arundinaceus*), is a high-quality cuckoo host (Kleven et al. 1999). We studied a dense cuckoo population in Hungary (>50% parasitism rate on Great Reed Warblers; Moskát and Honza 2002, Zölei et al. 2015), where cuckoos parasitize this host species breeding in the narrow reed-beds of small channels, surrounded by woodland patches and extensive agricultural areas. In the present study, we report and analyze our results for home range size estimation of Common Cuckoos in their breeding grounds through the application of non-PTT GPS methods.

We predicted that the non-PTT GPS method would generate accurate datasets on cuckoos' geographic positions which would allow for more reliable estimation of their home range sizes than other methods used previously. Earlier studies suggested that feeding areas and laying areas of Common Cuckoos do not always overlap during the breeding season (Vogl et al. 2004, Nakamura

et al. 2005). Such a bimodal use of disconnected habitats has also been reported for the Brown-Headed Cowbird (e.g., Rothstein et al. 1984, Curson et al. 2000). However, we predicted that in areas with high cuckoo density, host-breeding territories would be packed tightly along narrow reed channel-side habitats, and so cuckoos may also overlap in their use of the breeding sites. In addition, we discuss some technical details of the use of non-PTT GPS tags for cuckoos and also give examples of the difficulties in home range estimation in this brood parasite.

Our previous behavioral study of individually VHF tagged cuckoos revealed that males held partially overlapping territories on the breeding grounds in Hungary (Moskát et al. 2017). There is a high level of multiple cuckoo parasitism in our study area (~36% of parasitized Great Reed Warbler nests were multiply parasitized by 2–4 cuckoo eggs; Moskát and Honza 2002), and each cuckoo eggshell in these multiply parasitized nests has a different phenotype (shape, size, background color and maculation). This implies that different females (c.f. Moksnes et al. 2008) are co-laying in the same host nests, and so we predicted that female cuckoos would have partially overlapping breeding/egg-laying areas at this study site.

More generally, we also hypothesized that male Common Cuckoos, despite their lack of playing a known role in nest searching (Wyllie 1981), would mirror the distribution and density of local females in the breeding season. We therefore then predicted high overlap in home ranges between the cuckoo sexes. We also assessed whether females preferentially use host-breeding areas of reed-beds in the afternoons, when parasitic eggs are laid by this species. Finally, we tested whether nocturnal roosting sites were non-randomly distributed between cuckoo breeding and foraging habitat patches.

METHODS

Study Area and Population
We conducted our research near the village of Apaj (47.1150°N, 19.0892°E) in central Hungary, ~40 km south of Budapest. In this area, Great Reed Warblers breed at high densities in narrow (2–5 m) reed-beds along small irrigation channels. This species is the only known host for Common Cuckoos at this study site (C. Moskát et al. personal observation). The local parasitism rate is unusually high among cuckoo populations (>50%; Moskát and Honza 2002) and has been stable across the last century (Zölei et al. 2015). The channel banks typically consist of a narrow row of deciduous trees (mainly poplars [*Populus* spp.] or black locust [*Robinia pseudoacacia*]) and shrubs. The surrounding areas are comprised of arable fields with some scattered hardwood forest (mainly common oak [*Quercus robur*]) patches and narrow, unpaved roads lined with trees. Water management of channels (reed burning, reed cutting, mud removing, bush and tree cutting) may cause between-year environmental perturbations and affect host availability in such habitats (c.f. Mérő and Zuljevic 2019).

GPS Telemetry
We caught cuckoos with 6 m tall and 10–15 m long mist nets using playbacks of the male "cu-coo" calls and female "bubbling" calls between 2014 and 2017, in the first part of their breeding season (from early May until early June), because the cuckoos of each sex are attracted to these playbacks. Mist netting of cuckoos was most successful in sites with bushes and small trees (not taller than the net height). We tagged 15 adult cuckoos (6 males and 9 females) with lightweight GPS tags (model: PICA; Ecotone, Gdynia, Poland). Most of them were monitored over 1 breeding season, but 3 individuals were tracked for 2 consecutive years (Table 1). In the first year of the study GPS tags were equipped only with solar-charging batteries, and 3 out of 6 tags did not yield any data. Later, we used the combination of GPS loggers with solar-charged and non-rechargeable batteries, which helped to provide the tags with power on cloudy days or when birds perched in dense tree foliage (Table 1). A tag weighed 5.6 g including batteries (~5% of a cuckoo's body weight, in agreement with the ≤5% weight rule; see the recommendation by Bridge et al. 2011) and we used a leg-loop harness made of Teflon-ribbon to affix it to the back of the subject (Bán et al. 2018). We observed the behavior and foraging of our tagged birds, as well as non-tagged cuckoos with binoculars, and did not note any unusual patterns or differences. The PTT GPS tags produced by Microwave (Columbia, Maryland, USA) have almost exactly the same weights as our GPS tags, and have been extensively used without difficulties on the same species of cuckoo (e.g., Willemoes et al. 2014, 2015, Hewson et al. 2016, Vega et al. 2016, Williams et al. 2016). We remotely downloaded data from the GPS tags, without having to re-capture the birds, from 30 to 150 m away through a bidirectional ultra high frequency connection using a base station (Ecotone). This connection also allowed us to reprogram GPS tag settings. For example, just prior to the migratory season, we increased the fixing intervals up to 30 or 60 min from 5 or 15 min to conserve the energy of the tag and prolong their operational time during migration (more details and migratory data are published in Bán et al. 2018).

Molecular Sexing
We identified the sex of captured cuckoos based on plumage characters (Svensson et al. 2010) and validated it by DNA analysis (Daniel et al. 2007) from blood samples taken from the brachial vein. DNA was extracted by homogenizing 10 μL of blood in 500 μL extraction buffer as per the protocol in Bereczki et al. (2014). Molecular sexing was carried out using the P2/P8 method described

TABLE 1. Summary table of GPS tags applied to cuckoos related to the breeding seasons in our study area.

No. of data set	ID of GPS tag	Type of tag	ID of cuckoo individual	Sex	Mass (g)	Deployment date	Last download of data within the same breeding season	GPS interval (min)	Total number of fixes received [a]
1	S14	Pica S	C1	M	116	May 19, 2014		5	0
2	S08	Pica S	C2	F	110	May 20, 2014	June 11, 2014	5	195
3	S21	Pica S	C3	M	123	May 23, 2014	May 24, 2014	5	4
4	S19	Pica S	C3	M		May 24, 2014	July 17, 2014	30	60
5	S19	Pica S	C3	M		April 26, 2015	May 20, 2015	30	28
6	SB22	Pica S&B	C3	M		May 28, 2015	June 17, 2015	60	399
7	S30	Pica S	C4	M	104	May 21, 2014		5	0
8	S02	Pica S	C5	F	104	May 23, 2014		10	0
9	SB21a	Pica S&B	C6	F	107	May 28, 2015	July 14, 2015	60	804
10	SB21b	Pica S&B	C6	F		May 08, 2016	May 20, 2016	60	208
11	SB25	Pica S&B	C7	F	96	June 1, 2015	June 4, 2015	60	61
12	SB23	Pica S&B	C8	F	102	May 21, 2015	June 4, 2015	60	229
13	SB26	Pica S&B	C9	M	131	June 4, 2015	June 25, 2015	60; 30 [b]	589
14	SB27a	Pica S&B	C10	F	97	June 4, 2015	July 8, 2015	60; 30 [b]	374
15	SB27b	Pica S&B	C10	F	102	May 21, 2016	July 14, 2016	30	970
16	SB29	Pica S&B	C11	F	104	June 4, 2015	June 4, 2015	30	11
17	SB30	Pica S&B	C12	F	105	June 4, 2015	June 7, 2015	60	56
18	SB24	Pica S&B	C13	M	122	May 10, 2017	June 8, 2017	15	1861
19	SB20	Pica S&B	C14	M	114	May 10, 2017	June 6, 2017	5	4501
20	SB28	Pica S&B	C15	F	110	May 10, 2017	June 12, 2017	5	5087

F = female, M = male; S = solar-powered, S&B = solar- and battery-powered.
[a] In the study period (between the starting day and last download of data).
[b] Setting of the frequency of collecting GPS positions in an interval was changed during the course of the study.

by Griffiths et al. (1998), following the amplification protocol in Bereczki et al. (2014). PCR products were loaded on a silver-stained polyacrylamide gel. The electrophoresis buffer systems and running conditions as well as the staining solutions were used according to Bereczki et al. (2005, see appendix 2, 4a) and An et al. (2009). Sexing was based on the banding pattern after visualization by white light. Sexing of a larger sample size of cuckoos caught in the study area for different purposes (24 males and 8 females) confirmed that the sex in these adult Hungarian Common Cuckoos can be identified accurately by plumage characters (sensu Svensson et al. 2010; Table 1). Briefly, all adult females captured had some rufous feathers, although plumage hue varied widely (from a few brownish feathers up to the fully hepatic morph). In turn, all strictly gray morph adult individuals proved to be genetic males.

Estimation of Home Range Sizes

As traditional home range estimators are suitable for home range size calculations using spatial data collected by GPS technologies (Kie et al. 2010), we applied 2 common methods for home range estimations: the minimum convex polygon (MCP) and the kernel density estimation (KDE) methods. Instead of considering the MCP 100% based on all GPS-points (Kenward 2001), we used its variant, the MCP 85% method (Kenward 2006, Blondel et al. 2009)

on 85% of GPS-points in the core areas of their clouds. This variant, also called the "core home range" method, is typically applied to exclude large areas rarely used by the animals (Bubela and Happold 1993). We also applied the KDE method where data were derived from an individual's Utilization Distribution (UD 85%). The bandwidth in KDE should be based on habitat (Kauhala and Autilla 2010) and the biological question (Kie et al. 2010). Therefore, we chose the 85% counter level and divided our home ranges into subunits as our locations are clumped into habitat patches (Figures 1 and 2). A home range by the KDE method was calculated as the sum of the estimations for each habitat patch of an individual cuckoo (Table 1). Our tags typically also collected single points from cuckoos that were probably commuting between habitat patches (typically over agricultural fields), as well as on their exploratory routes, which were treated as outliers when the 85% contour level was applied. Home range analyses were performed using the R statistical environment (R Core Team 2017), with the AdehabitatHR package (Calenge 2015).

Statistical Analyses

We used SPSS 17 for statistical analyses other than home range estimation (see above). When 2-year data were available from an individual cuckoo, we used only one of them in statistical analyses to avoid pseudoreplication: we analyzed the year when more fixes were available. Accordingly,

we used data from 2015 for cuckoos ID = C3 and ID = C6, and used data from 2016 for cuckoo ID = C10; see Tables 1 and 2 for cuckoo IDs). As Seaman et al. (1999) suggested, we used data from cuckoos where at least 50 fixes were collected by the GPS logger (Table 2). We omitted individuals with <100 fixes when daily habitat uses were evaluated (ID = C7 and ID = C12; Figure 3). When we compared night usage of channel-side and woodland habitats, this estimation was based on percentages of fixes from the 2 habitats per individual between 2100–2200 hours and 0400–0500 hours local night time period. In the same way

we quantified daily habitat use in channel-side and woodland habitats, standardized for the 0500–2100 hours daylight period. For females we also compared habitat use in the mornings (0500–1100 hours) and in the afternoons (1500–2100 hours).

RESULTS

Home Range Sizes of Common Cuckoos
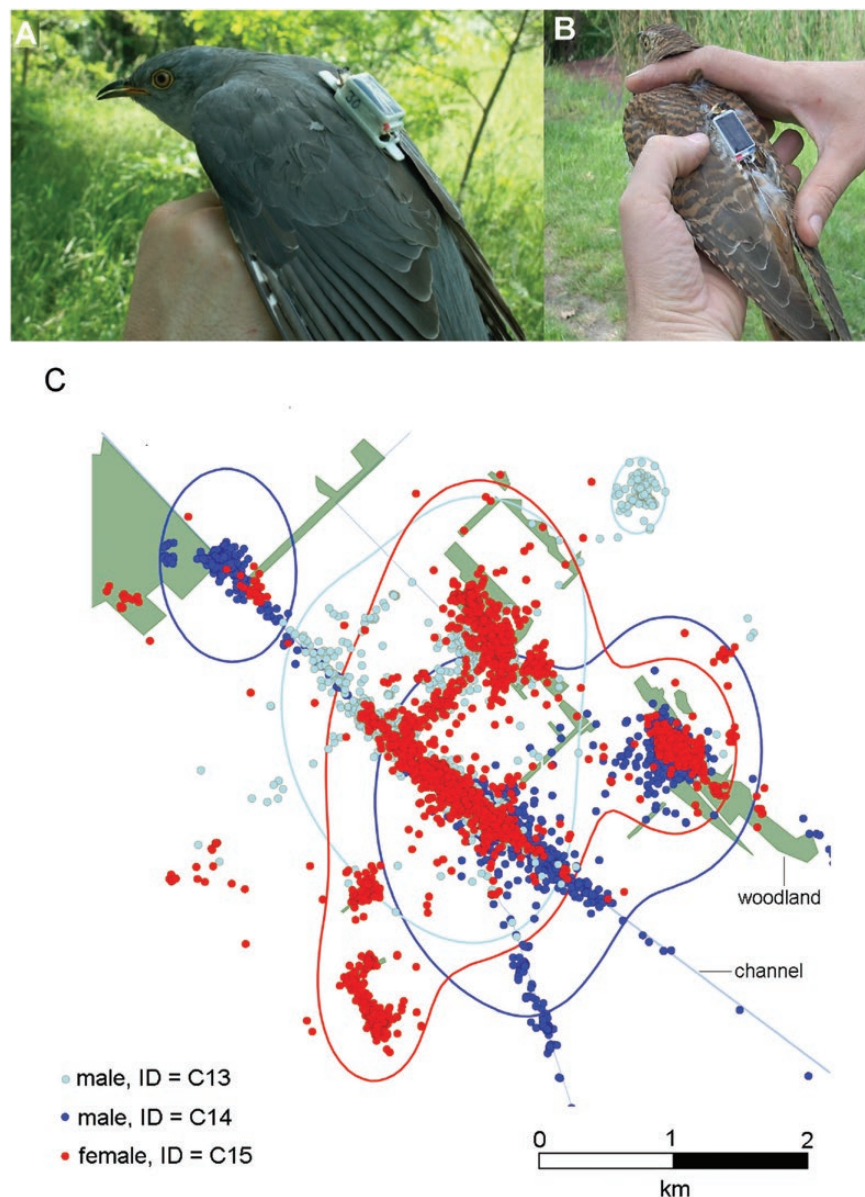The majority (71.4%) of the tagged cuckoos (*n* = 14) had bimodal habitat use (channel-side reed-bed and woodland

FIGURE 1. Adult (**A**) male and (**B**) female Common Cuckoo equipped with remote-downloadable non-PTT GPS tags (photos courtesy of Miklós Bán and Csaba Moskát, respectively). (**C**) Map of actual detection points and calculated home ranges of 2 males (with distinct patches) and 1 female cuckoo (continuous) with overlapping distributions from 2017, based on the kernel density estimation (UD 85%) method.
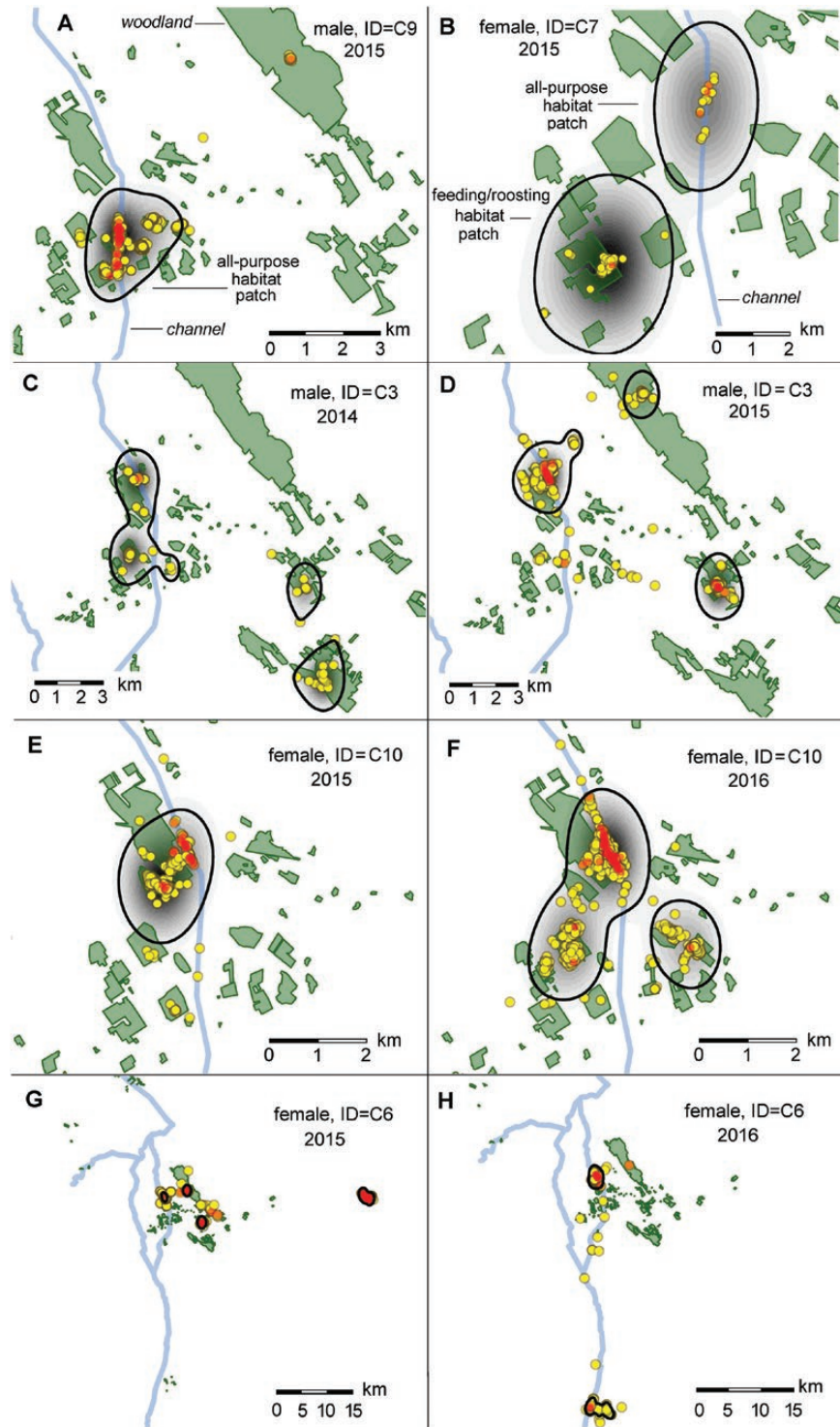
FIGURE 2. Examples of habitat and patch use by Common Cuckoos, where their hosts, Great Reed Warblers, nest in the reed-beds of small channels. (Blue lines = channels, green patches = woodlands, white background = arable fields.) (**A**) An example of unimodal habitat use by a male cuckoo. (**B**) An example of bimodal habitat use by a female cuckoo. Home ranges of a male (**C, D**) and 2 female cuckoos (**E**, **F**) and (**G**, **H**) were from 2 consecutive years and estimated by the kernel density estimation (UD 85%) method.

and channel-distant woodland), whereas 28.6% restricted their movements to the channel-side reed-bed host-breeding habitat (Table 2). When cuckoos used multiple habitat patches the largest distances between the centroids of habitat patches used by individual cuckoos varied widely (median = 8.3 km; range: 2.2–39.5 km; n = 10; Table 2). In general, an individual had a larger home range when it used more habitat patches than a single patch (UD 85% method, Spearman's rho = 0.83, P = 0.002, n = 11; Table 2). Moderate (>50) or large (thousands) sample sizes of locations seemed to be similarly efficient in home range size and modality estimations, as the number of fixes used for the estimation of home ranges correlated neither with home range sizes calculated by KDE (UD 85%) method (Table 2; Spearman's rho = 0.21, P = 0.54, n = 11), nor with the number of separate patches used (Spearman's rho = −0.15, P = 0.67, n = 11). Indeed, the cuckoo (ID = C15) that received the greatest number of fixes (5,087) had a unimodal habitat use (Table 2).

Home range estimations by the MCP 85% method appeared to be unrealistically high on occasion (Table 2). This method gave the highest estimations in 6 of 14 cases from the 2 methods tested (i.e. the MCP 85% and UD 85% methods), and in the rest of cases (8 of 14) the KDE (UD 85%) gave the largest estimations (Table 2). There were no significant intra-individual differences for the estimations by the MCP 85% and UD 85% methods (Wilcoxon signed rank test, z = −0.09, P = 0.93, n = 11).

Characteristics of Cuckoo Home Ranges

Most cuckoos spent the night in a single habitat (channel or woodland) and had no bias between these habitats (Wilcoxon signed rank test based on an individual's percentage of their stay in the 2 habitats: Table 3; z = −0.09, P = 0.93). A similar lack of differential pattern was observed in daytime habitat choice among cuckoos (Wilcoxon signed rank test: z = −0.14, P = 0.89). Cuckoos typically moved short distances, as consecutive locations recorded by the GPS loggers only exceptionally were >1 km. This pattern seemed to be stable at all times of the day during which cuckoos were tracked (Figure 3). Our data showed that cuckoo females spent significantly more time in the reed-beds than in woodland patches in the afternoons (median = 78.1%; range: 11–100%) than in the mornings (30.3%; 5.2–54.5%) (Wilcoxon signed-rank test: z = 2.24, P = 0.02).

Our maps had high overlap between male and female home ranges (see e.g., Figure 1C). The numbers of distinct habitat patches used by the 2 sexes were also similar (median and range: males: 2 (1–3); females: 2 (1–4); Mann-Whitney U-test: $U_{7,4}$ = 12.0, P = 0.798), and overall sizes of their home ranges (measured by the UD 85% method) were similar for the 2 sexes (median and range: males: 6.5 km² (5.5–12.8); females: 8.7 km² (0.8–14.3); $U_{7,4}$ = 11.0, P = 0.65). When we compared the relative frequencies of fixes of female and male cuckoos located in channel-side habitats (as opposed to staying in woodland patches), we detected no statistical difference (Mann-Whitney U-test, $U_{7,4}$ = 6.0, P = 0.16).

TABLE 2. Estimations of Common Cuckoo home ranges by minimum convex polygon (MCP 85%) and the kernel density estimations where data are derived from each individual's utilization distribution methods (UD 85%). Cluster 1 in UD 85% estimation shows the potential laying area of female cuckoos, where Great Reed Warbler hosts were presented, except for cuckoo C6-2 where both clusters 1 and 2 were potential laying areas.

Cuckoo ID	Sex	Year	No. of GPS fixes [a]	MCP 85% home range (km²)	No. of polygons	UD 85% home range (km²) (sum of parts)	UD 85% home cluster 1 (km²)	UD 85% home cluster 2 (km²)	UD 85% home cluster 3 (km²)	UD 85% home cluster 4 (km²)	Largest distance of centroids (km)
C2	F	2014	195	10.2	3	8.7	4.3	4.0	0.3	-	8.0
C12	F	2015	56	0.3	1	0.8	0.8	-	-	-	-
C9	M	2015	589	1.6	1	5.5	5.5	-	-	-	-
C3-1	M	2014	64	39.0	3	16.8	9.7	2.6	4.6	-	10.4
C3-2	M	2015	427	51.8	3	12.8	6.4	2.2	4.2	-	8.7
C8	F	2015	229	13.7	3	9.3	4.6	3.0	1.6	-	9.3
C10-1	F	2015	374	0.7	1	4.0	4.0	-	-	-	-
C10-2	F	2016	970	8.6	2	8.8	6.7	2.1	-	-	2.3
C6-l	F	2015	804	151.1	4	14.3	1.5	2.5	3.2	7.1	39.5
C6-2	F	2016	208	185.5	2	15.0	8.4	6.7	-	-	35.9
C7	F	2015	61	1.7	2	5.9	3.5	2.4	-	-	2.5
C13	M	2017	1861	2.1	2	6.0	5.8	0.2	-	-	2.2
C14	M	2017	4501	3.7	2	7.1	5.9	1.1	-	-	3.0
C15	F	2017	5087	7.6	1	7.8	7.8	-	-	-	-

[a] Numbers of fixes are shown from the breeding area only; F = female; M = male; MCP = minimum convex polygon; UD = kernel density estimation (KDE) method, derived from individual's utilization distribution; individual C11 was also omitted from calculation of descriptive statistics and from statistical tests because of low number of fixes supplied; C3-1, C10-1 and C6-2 were not used in statistical analyses to avoid pseudoreplication.
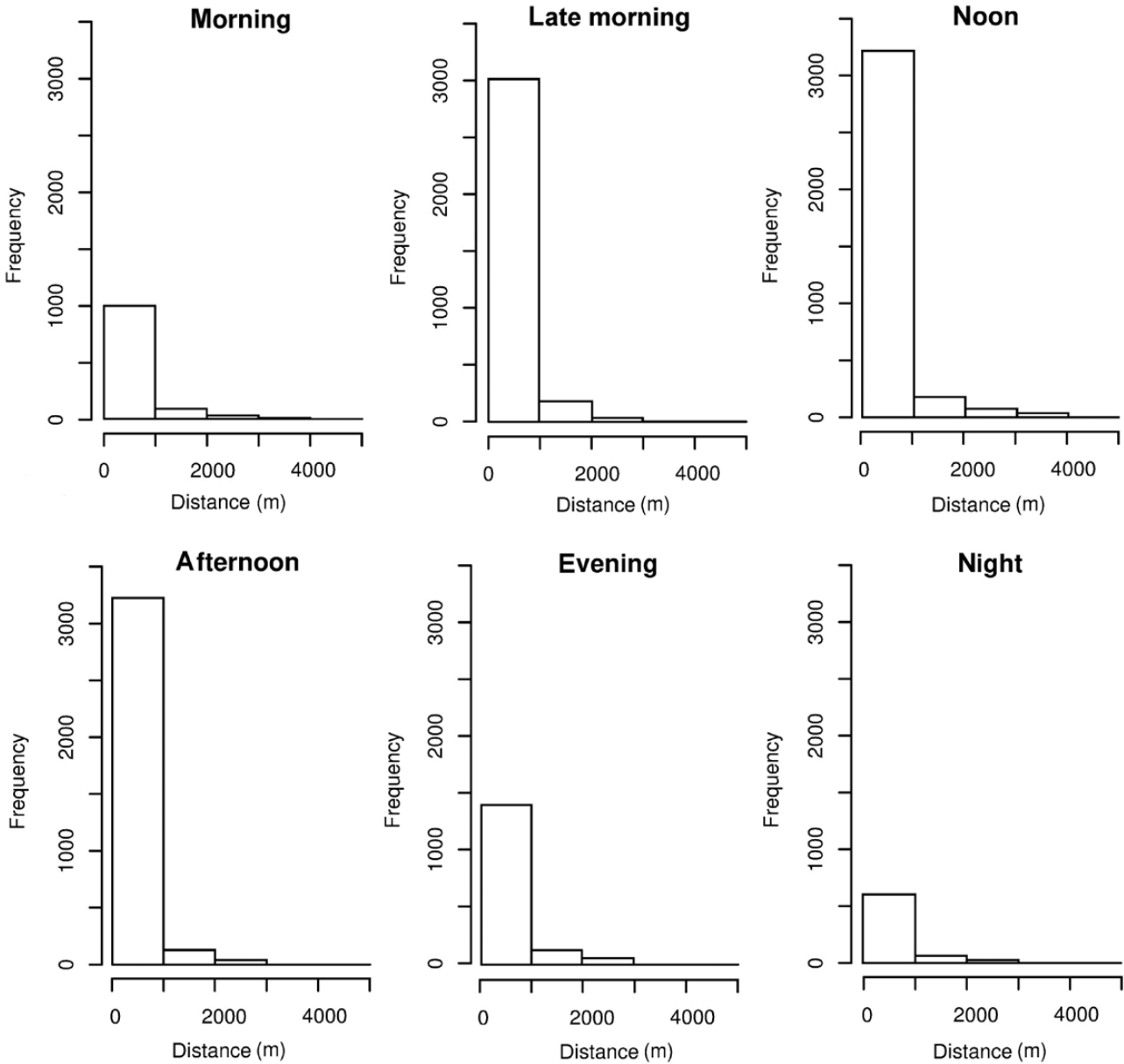
FIGURE 3. Daily pattern of movement lengths of cuckoos based on consecutive GPS positions (morning: 0500–0700 hours Central European Time (CET); late morning: 0700–1100 hours; noon: 1100–1500 hours; afternoon: 1500–1700 hours; evening: 1700–2100 hours; night: 2100–2200 hours and 0400–0500 hours; based on cuckoo IDs C2, C3-2, C8, C9, C10-2, C13, C14 and C15).

We observed and downloaded data from 3 cuckoos in the subsequent year in the same area as they were previously captured and tagged (see above, Figure 2C–H). Although the breeding areas of home ranges of these cuckoos were similar, their boundaries and foraging patches partly changed. In 2017, we also observed 2 cuckoos in our study site with backpacks probably tagged ≥2 yr ago, but we could neither capture them nor download their data.

TABLE 3. Cuckoos habitat use (%) daytime and at night (on cuckoos where number of fixes obtained by the GPS tag >100).

	Channel daytime	Woodland daytime	Channel at night	Woodland at night
Median	60.8	39.2	49.2	50.9
Minimum	2.9	0.0	0.0	0.0
Maximum	100.0	97.1	100.0	100.0
N	8.0	8.0	8.0	8.0

DISCUSSION

Bimodal Use of Habitat Types?

Previous studies using VHF telemetry revealed that adult Common Cuckoos use 2 types of habitat during the breeding season (Dröscher 1988, Nakamura and Miyazawa 1997, Vogl et al. 2004): one is for mating and breeding, and the other is for feeding and roosting. Our study in central Hungary, using a miniature GPS tracking method, confirmed the bimodal habitat structure of parasitic cuckoos' home ranges, using a novel application of the tracking method. This allowed for gathering larger quantities and more detailed data on the cuckoos' movements within and between their breeding and foraging areas, without being limited by the observer's capacity in tracking and by triangulation problems that arise when VHS telemetry is used. Home ranges in both types of habitat were characterized as multipurpose use of habitat patches, varying in size and consisting of 1–4 compartments for an individual cuckoo. In our study area, the Great Reed Warbler is the cuckoo's primary (seemingly exclusive) host species, and the parasitism rate is high (Moskát and Honza 2002). Great Reed Warblers breed in reed-beds along small channels, typically bordered by rows of trees or woodland patches, serving as good perching sites for cuckoos preferring tree canopy roost sites, which act as view points for nest-searching and host-observation by female brood parasites (Moskát and Honza 2000).

Female cuckoos typically search for more host nests than they eventually parasitize (Nakamura et al. 2005) and show flexibility in nest-searching tactics depending on host density (Jelinek et al. 2014). Female cuckoos are cognitively specialized to be a nest parasite: they acquire and recall information about host nest locations and breeding stages. Although obligate brood parasitic cuckoos have smaller brain sizes than do non-parasitic cuckoos (Payne 2005, Boerner and Krüger 2008), spatial information is specifically stored and requires preferential anatomical investment in the hippocampus (O'Keefe and Nadel 1978). Consistent sex-differences in relative hippocampal volumes of female vs. male cuckoos are not yet known (Davies 2011), but such volumes are significantly larger and hippocampal neurogenesis levels are greater in female brood parasitic cowbirds than in males, suggesting neuroanatomical specialization for spatial memory storage and retrieval in at least one brood parasitic lineage (Sherry et al. 1993, Reboreda et al. 1996, Guigueno and Sherry 2017).

Common Cuckoos in some Japanese populations lay in host nests located in reed-beds, using the Oriental Reed Warbler (*A. orientalis*) as their primary host species, but they spend most of their time, including night time, in nearby montane forests (Nakamura and Miyazawa 1997). In our study, Hungarian cuckoos spent about half of their daytime in the close vicinity of channel-side reed-beds, but they also visited nearby woodland patches, presumably for feeding and roosting (up to 40 km distance) during daytime hours. Specifically, female cuckoos were more likely to stay in reed-beds in the afternoons than in the mornings, which is consistent with their behavior of typically laying eggs in host nests in the afternoons (Davies and Brooke 1988). Regarding nocturnal roosting, Hungarian cuckoos spent their nights either at the channels or in the woodland patches, without any clear preference for either. Our study thus revealed the necessity of assigning cuckoos' occurrences within each of the 2 types of habitat patch independently from each other, as the simple geometric combination of these GPS fixes into a single home range, including inter-patch areas, would have resulted in unrealistically vast home range estimations for individuals in this cuckoo population.

Furthermore, our study demonstrated that the structure of cuckoos' home ranges had high variability, both in home range sizes (from 1 to 17 km^2 estimated by the 85% KDE), unimodal (29% of individuals tracked) or bimodal (71%) habitat patch use, and also in the range of the longest inter-patch distances of individual cuckoos engaged in multimodal habitat use (between 2 and 40 km). We also revealed that uni- or bimodal habitat use was not a simple consequence of low or large sample sizes (i.e. not a positive function of the number of fixes collected by our GPS tags per individual).

Methodological Remarks

Unrealistic home range sizes? In patchy landscapes, home range estimation is technically not straightforward, because unused intervening areas may increase the estimated home range size beyond the biologically meaningful usage area (Mitchell and Powell 2008). In this study, we applied 2 different methods, the MCP and the KDE approaches for the calculation of cuckoo home range sizes (Table 2). We identified multiple habitat patches used through the KDE method, and total home range sizes were calculated as the sum of patch sizes for each individual. We did not include spatially isolated points of occurrence. Such coordinates received by GPS tags seem to be points far from their habitat patches used. These outliers are not due to inaccuracy of GPS estimates, but they would also increase home range estimates by the MCP method. There are 2 possible explanations for these distant, singly spaced points: (1) if they fell between 2 patches, these GPS coordinates had been recorded when the birds were flying from one patch to the other; or (2) single or low-number clustered points is the explorative behavior of cuckoos, which would be adaptive for both female and male cuckoos during the breeding season. Occasionally, cuckoos in our study site were spotted several km away from their typical

home ranges, perhaps searching for new host nests and for new mating partners.

If cuckoos used a channel-side reed-bed section with narrow woodlands along the banks, this appeared as a quasi-linear home range along the channel (e.g., Figure 2B), and so the elliptical home range estimated by the KDE method yielded larger ranges than the actual area used by cuckoos (c.f. Figure 2B). However, other effects might also cause bias in estimation. Some home ranges were surprisingly large, especially by the MCP estimations and when cuckoos used multiple patches (Table 2). An example of this rare case was cuckoo ID = C6, where the area of convex polygons (MCP 85%) was roughly 15x higher than that of the KDE (UD 85%; Table 2).

We consider that in most cases the KDE method gave a more reliable estimation than the MCP method (UD 8.8%: mean = 8.8 km^2; MCP 85%: mean = 34.1 km^2). A previous study on Common Cuckoos in contiguous Czech fish-ponds with reed-beds revealed small territories of cuckoos (median = 0.6 km^2; Vogel et al. 2004). However, that study was conducted in a habitat different from our study and used the traditional VHF telemetry, where the observers had a limited ability to follow each bird during entire days, especially to more distant off-pond foraging or roosting locations. This may cause the underestimation of actual home range sizes in VHF studies. The largest cuckoo home range size estimation was calculated for breeding home ranges of cuckoos in Scandinavia by the KDE 95% method (mean ± SD: 135 ± 70 km^2; Williams et al. 2016), but that study used the PTT satellite GPS method, a typically less accurate method than the non-PTT GPS technique (Bán et al. 2018).

Technical suggestions.   As our study was the first to use the non-PTT GPS method for characterizing the home range sizes in breeding parasitic birds, we experimented with applying different settings to test for the most appropriate data collection parameters of the Ecotone's Pica GPS tag system and set-up. We found that the tags with mixed power supply (both solar-charged and non-rechargeable batteries) worked better, whereas exclusively solar-charged tags sometimes failed. If cuckoos stayed under dense foliage while perching on trees, fed in closed canopy forests, or moved about in cloudy weather, the solar charger alone appeared insufficient to power data collection and archiving by the GPS tag.

Future studies.   Additional work should focus on the factors covarying with and causing the high flexibility of parasitic cuckoo home ranges. Factors to assess could include the timing of the availability of host nests (Moskát et al. 2006), seasonal home range shifts and dynamics, and the exploratory behavior of cuckoo females searching for new host nests and host-breeding sites when facing a shortage of active local nests suitable

for parasitism (Geltsch et al. 2016). Given that female cuckoos also have overlapping home ranges, another question could be related to whether and how females share or compete for critical resources (e.g., active host nests). Further studies in Hungary and elsewhere should also address the relationship between female vs. male spacing patterns and their role in shaping the cuckoos' genetic mating system. The known polygynandrous mating system of Common Cuckoos in the UK and Japan (Wyllie 1975, Marchetti et al. 1998) appears to be favored by overlapping territories of males with one or more laying areas for female cuckoos, a spacing pattern that we also detected in our study population. Finally, the non-PTT GPS method used to track cuckoos allowed us to observe a handful of cases of inter-annual breeding philopatry of cuckoos, as had been noted by cuckoo studies previously (Chance 1940).

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