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CHEATING CHEATERS: SOCIAL MONOGAMY BUT GENETIC POLYGAMY IN A BROOD PARASITE

ENGAÑANDO A LOS TRAMPOSOS: MONOGAMIA SOCIAL PERO POLIGAMIA GENÉTICA EN UN PARÁSITO DE CRÍA

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SUMMARY.—Understanding the variability of mating systems is central in the study of animal behaviour. The advent of genetic techniques allowed combining social and genetic data, providing a more comprehensive view of reproductive strategies. In obligate avian brood parasites, the lack of constraints derived from offspring care allows for great plasticity of the mating system in response to changes in socio-ecological conditions. This potential for intraspecific variation makes brood parasites ideal model species to investigate the evolution of reproductive behaviour. We simultaneously studied for the first time social and genetic patterns of reproduction of the Great Spotted Cuckoo *Clamator glandarius*, combining radio-tracking and behavioural observations in the field with genetic parentage analyses. Our results reveal that loose pair bonds can be maintained in this species despite high levels of genetic polygamy and lack of territoriality, possibly because of the need of intra-pair cooperation for finding and parasitising the nests of its large hosts: the Carrion Crow *Corvus corone* and the Eurasian Magpie *Pica pica*. We also found that cuckoos mostly ranged around suitable foraging grounds, but females moved larger distances to find host nests to parasitise. Comparison of our results with previous reports on different populations also suggests a plasticity of Great Spotted Cuckoo territorial behaviour that may depend on population density, host choice and distribution of host nests. —Bolopo, D., Roncalli, G., Canestrari, D. & Baglione, V. (2020). Cheating cheaters: social monogamy but genetic polygamy in a brood parasite. *Ardeola*, 67: 39-56.

Key words: *Clamator glandarius*, Great Spotted Cuckoo, home range, pair bonds, social interaction, territoriality.

RESUMEN.—Entender la variabilidad de los sistemas de apareamiento es un aspecto crucial del estudio del comportamiento animal. El uso de técnicas moleculares ha permitido combinar observaciones del comportamiento social con datos genéticos para obtener una visión más completa de las estrategias

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reproductoras. En los parásitos obligados de cría, la falta de limitaciones derivadas de los cuidados parentales permite una mayor plasticidad del sistema de apareamiento en respuesta a las condiciones socioecológicas. Este potencial para la variación intraespecífica hace de los parásitos de cría excelentes modelos de estudio para investigar la evolución del comportamiento reproductor. Estudiamos por primera vez simultáneamente los patrones sociales y genéticos de la reproducción del críalo europeo *Clamator glandarius*, combinando radioseguimiento, observaciones de campo y análisis genéticos de paternidad. Nuestros resultados revelan que unos vínculos laxos de pareja pueden mantenerse en esta especie a pesar de altos niveles de poligamia genética y ausencia de territorialismo, posiblemente como consecuencia de la necesidad de cooperación de la pareja para parasitar los nidos de sus robustos hospedadores (la corneja negra *Corvus corone* y la urraca *Pica pica*). También encontramos que los críalos radiomarcados se movían preferentemente por los alrededores de las áreas de forrajeo, aunque las hembras podían realizar largos desplazamientos para encontrar nidos de hospedadores. La comparación de nuestros resultados con estudios previos en diferentes poblaciones también sugiere una plasticidad en el comportamiento territorial del críalo, que puede depender de la densidad de la población, la elección del hospedador y la distribución de sus nidos. —Bolopo, D., Roncalli, G., Canestrari, D. y Baglione, V. (2020). Engañando a los tramposos: monogamia social pero poligamia genética en un parásito de cría. *Ardeola*, 67: 39-56.

Palabras clave: área de campeo, *Clamator glandarius*, críalo europeo, interacción social, lazos de pareja, territorialismo.

INTRODUCTION

Monogamy was accepted as the prevalent mating system in birds (Lack, 1968) until molecular techniques showed a different scenario. Extra-pair paternity in socially monogamous species has been detected in about 76% of the more than 250 species where genetic techniques have been used to determine paternity (reviewed by Brouwer & Griffith, 2019), showing that social patterns only weakly predict the number of sexual mates. Reproductive social relationships, however, remain a fundamental component of a species' mating system. Indeed, the selective processes that culminate in a given distribution of sexual mates can be fully understood only if the behavioural strategies at individual level; e.g. strength of within-pair social bonds, male mate guarding, intra and intersex competition, etc., are considered (Carranza, 2016). Therefore, ideally, social and genetic information should always be combined when investigating the breeding biology of birds.

Avian brood parasites, which lay their eggs in the nests of other species and have their

offspring raised by foster parents (Davies, 2000), present a unique opportunity for testing the theory of evolution of mating systems (Kruger, 2007). These species are freed from most of the social, ecological and temporal constraints of parental care, and are therefore predicted to show a variety of key differences from nonparasitic species (reviewed by Hauber & Dearborn, 2003; Feeney & Riehl, 2019). Briefly, brood parasites may show 1) higher levels of both polyandry and polygyny as the lack of parental duties reduces the benefits of pair bonds, and 2) larger plasticity of mating strategies, which may adjust quickly to ecological and social current conditions (e.g. population density, host-species composition, etc.). Monogamy, however, could also be selected for, particularly when female-male cooperation increases egg laying success, either by facilitating the host nest location or by circumventing host defences against the parasite.

The degree of territoriality can also have important consequences on the mating system in both parental and parasitic species. Indeed, the strength of defence of home range

boundaries may influence the probability of encounters among multiple potential sexual partners (Emlen & Oring, 1977; Hauber & Dearborn, 2003; Feeney & Riehl, 2019), leading to monogamy when territories are exclusive, or polygamy when home ranges largely overlap. Territoriality in brood parasites depends on the distribution and defensibility of both food resources and host nests, and therefore on the degree of spatial coincidence between feeding areas and host breeding areas. Decoupling of these areas may preclude effective exclusion of intruders, leading to non-territoriality (Martínez *et al.*, 1998). The situation complicates further when the parasite can target different host species, if they differ in the distribution of their nests. Theory predicts that when resources (host nests, in this case) are patchily distributed, they are easier to monopolise and defend than when they are distributed evenly (Davies *et al.*, 2012). Under this scenario, parasite territorial behaviour, and hence the encounter rate between potential sexual partners, will also depend on host choice. Studying brood parasite territoriality, and the factors that drive it, has therefore important implications for understanding their mating patterns.

In spite of the interest of studying brood parasites for understanding the transitions between different mating systems (Kruger, 2007), research on brood parasites has focused primarily on testing the predictions of co-evolutionary arms race theory, neglecting their natural history and, specifically, their reproductive and territorial behaviour (Feeney *et al.*, 2014; Soler, 2014). This is due, at least in part, to the difficulties of their study. On the one hand, the lack of a reference point (the nest) for behavioural observations and the absence of conspicuous breeding behaviours (such as nest building, egg incubation and chick provisioning) hinder the characterisation of the social relationships between putative reproductive partners. On the other hand, genetic data are also difficult

to collect because parents may have their offspring dispersed in many host nests over large areas that are difficult to sample. Furthermore, a comprehensive view of the mating system of a brood parasite species can only be achieved if social and genetic data are concurrent, because the expected behavioural plasticity of these species invalidates merging information from studies that are separated temporally or geographically.

Due to this complexity, the literature on the mating systems and territorial behaviour of avian brood parasites is particularly scant, hindering a comprehensive test of some key predictions of mating system theory. Colour-banding studies have reported on promiscuous or polygamous mating in the Orange-rumped (Yellow-rumped) Honeyguide *Indicator xanthonotus* (Cronin & Sherman, 1977), Village Indigobird *Vidua chalybeata* (Payne & Payne, 1977) and Pintailed Whydah *Vidua macroura* (Barnard & Markus, 1989). Radio-tracking techniques, especially on breeding females, have been used to study habitat use and territoriality on Common Cuckoo *Cuculus canorus* (Nakamura & Miyazawa, 1997; Vogl *et al.*, 2002, 2004; Nakamura *et al.*, 2005; Moskát *et al.*, 2019), Brown-headed Cowbirds *Molothrus ater* (Rothstein *et al.*, 1984), Shiny Cowbirds *Molothrus bonariensis* and Screaming Cowbirds *Molothrus rufoaxillaris* (Scardamaglia & Reboreda, 2014). The latter found that male and female Screaming Cowbirds that were trapped together showed a certain degree of social bonding during radio-tracking, suggesting social monogamy. A few molecular studies have been also carried out to describe genetic mating patterns, as well as egg laying ranges, of the Common Cuckoo (Jones *et al.*, 1997), the Great Spotted Cuckoo *Clamator glandarius* (Martínez *et al.*, 1998; Martínez *et al.*, 1998), the Brown-headed Cowbird (Alderson *et al.*, 1999; Strausberger & Ashley, 2003) and the Horsfield's Bronzecuckoo *Chalcites basalus* (Langmore *et al.*,

2007). Contrasting results from different genetic studies of the same species showed evidence of temporal and/or geographical variation in the levels of genetic polygamy (see Jones *et al.*, 1997 and Marchetti *et al.*, 1998 for the Common Cuckoo, Martínez *et al.*, 1998; Bolopo *et al.*, 2017 for the Great Spotted Cuckoo and Alderson *et al.*, 1999 and Woolfenden *et al.*, 2002 for the Brown-headed Cowbird), highlighting once more the need for concurrent social and genetic data to fully understand the mating systems of brood parasites.

In this study we address the relationship between genetic and social mating system in brood parasites, using the Great Spotted Cuckoo as the model species. This migrant non-evicting cuckoo species specialises in parasitising corvids, the Eurasian Magpie *Pica pica* being the primary host in most Palearctic populations, and the Carrion Crow *Corvus corone* the secondary host (Soler, 1990). Host choice, however, can reverse under particular ecological conditions, as occurs in our study area where the Great Spotted Cuckoo prefers crow nests (Baglione *et al.*, 2017). Flexibility of the genetic mating system has been reported in this species, with the degree of polygamy varying temporally and geographically, most likely as a consequence of population density (Martínez *et al.*, 1998; Martínez *et al.*, 1998; Bolopo *et al.*, 2017). The social mating system and territorial behaviour of this species, however, is largely unknown. Early reports by Arias de Reyna *et al.* (1987), based on recorded movements of unbanded individuals, categorised this species as territorial in the Sierra Morena (southern Spain), whereas a more recent genetic study (Martínez *et al.*, 1998) showed a large overlap of female laying ranges at Guadix (southern Spain). Rühmann *et al.* (2019) also found no territoriality of GPS-tagged individuals during both the breeding and non-breeding seasons.

The Great Spotted Cuckoo may face counteracting pressures leading to either social monogamy or polygamy, making this species a valuable model for investigating the ecology of avian mating systems. The parasitic habit should reduce selective pressure for social monogamy (Hauber & Dearborn, 2003) but, conversely, the Great Spotted Cuckoo may need cooperation between sexual partners, and therefore pair bonds, for a) finding host nests, which is more demanding for a specialist brood parasite, than for generalists (Hauber & Dearborn, 2003), b) overcoming the defences of magpies, which mob the parasite and actively defend their nests (Soler *et al.*, 1999), and c) increasing vigilance at crow territories to enhance detection of temporally unattended nests, which is essential for parasitising such a large host (Canestrari *et al.*, 2009). In this study, we explored the outcome of this complex interaction and provide a comprehensive view of the Great Spotted Cuckoo mating system, by combining parentage analysis (reported in Bolopo *et al.*, 2017) with concurrent radiotracking data that address its home range characteristics, territorial behaviour, habitat use and sexual social bonds.

METHODS

Study site

The study was carried out in a 45km² rural area in northern Spain (42°37'N, 5°26'W, Sobarrriba, León). The area is characterised by a low-intensity agricultural landscape comprised by a mosaic of crops, meadows, riparian vegetation, poplar *Populus* sp. and pine *Pinus* sp. plantations, scattered shrubs, Pyrenean Oak *Quercus pyrenaica* forest patches, isolated trees and small patches of Holm Oaks *Quercus ilex*, and uncultivated land.

The Great Spotted Cuckoo is migratory in the study area and arrives to breed at the end of winter or early spring (March-April). Unlike other Iberian populations, the Carrion Crow *Corvus corone* is the main host at our study site, whereas the Eurasian Magpie *Pica pica* is the secondary host (Baglione *et al.*, 2017). In this part of Spain, crows breed cooperatively in about 75% of territories, building open nests in the upper third of the trees. They may re-nest up to twice per season in the event of early nest failure (Canestrari *et al.*, 2010). Magpies breed in unassisted pairs, build roofed nests hidden in brambles, scrubs, thorny bushes and occasionally in trees, and may re-nest once after a breeding failure (Birkhead, 1991). Both hosts place their nests at the edge of oak forests, in small tree patches or on isolated trees or bushes.

Field data collection

In March-April 2009 and 2010, we captured cuckoo adults by call playback and mist-netting in feeding areas (pine plantations). Each individual was marked with numbered metallic rings, measured and bled (~100–200 µl) from the brachial vein for sexing and parentage analyses (see Bolopo *et al.*, 2017 for complete description). Cuckoos were fitted with radio transmitters Holohil BD-2 that weighed 1.6g (~1% cuckoo average weight), attached to the two central tail feathers. After release, all captured birds were relocated in randomised order between 7am and 5pm UTC time, once or twice per day, from May 1st in 2009 and April 1st in 2010. The variation in the start of the relocation dates was due to logistic constraints for fieldwork in 2009. We relocated the birds with a directional antenna and a Followit RX98 receiver. We used the homing method (Fuller *et al.*, 2005) for radio-tracking and, for each location, we established visual and acoustic contact with the tagged birds to pre-

cisely identify the habitat used and to record the social circumstance (alone, together with another tagged/untagged bird). Although this time-consuming procedure inevitably constrained the number of locations we could obtain for each bird, it provided the fine-scale information that was necessary to fulfil the aim of this study. When the individual was accompanied by a conspecific, we also noted how they interacted (sitting together/moving co-ordinately/vocalising reciprocally *versus* chasing/ignoring each other). All locations were recorded in high resolution geo-referenced aerial photographs that enabled marking the exact positions of the cuckoos (up to 50cm accuracy).

We surveyed all crow and magpie nests in the study site from the end of March until the end of the breeding season (end of June) in 2009 and 2010. For each nest, we recorded laying date, hatching date, hatching success and fledging success for both hosts and parasite. When the clutch was found already complete, we visited the nest every 2–3 days to estimate hatching date and therefore laying date (incubation periods of crow, magpie and cuckoo eggs are 19–20, 17–18 and 13–14 days respectively; Canestrari *et al.*, 2017; Álvarez & Arias de Reyna, 1974; Cramp & Perrins, 1994). When cuckoo chicks were four days old we obtained a small sample of blood (50–100 µL) from their brachial vein for parentage genetic analyses (see details in Bolopo *et al.*, 2017).

We captured and radio-tagged 11 adult cuckoos in 2009 (eight males, three females) and 13 adult cuckoos in 2010 (eight males, five females). One of the females captured in 2009 returned the following year; she was recaptured and radio-tagged, but disappeared from the study area before we could record any movement. On four occasions we captured two individuals in the net at the same time: one male-male (MM) and one male-female (MF) dyad in 2009, and two MF dyads in 2010. Nineteen birds (12 males and

seven females) were radio-located until their death (three predated, one drowned in a well and one cause unknown), the disappearance of the radio signal ($N = 7$) or the end of the seasonal fieldwork ($N = 7$). The other five birds were never located again after capture, one due to predation and the rest most likely because they moved out of our study site. We surveyed 70 crow and 63 magpie nests in 2009, and 61 crow and 50 magpie nests in 2010, including second clutches; of these, 46, 10, 43 and 9 respectively were parasitised by Great Spotted Cuckoo.

Data analysis

Mapping

We elaborated a detailed habitat map at scale 1:3000 from geo-referenced aerial photographs using ArcGis 10 (ESRI, 2014). We categorised five habitat types: 1) “pines”: pine plantations; 2) “forest”: forest or plantations formed by trees other than pines, such as poplars, oaks or mixed formations; 3) “riparian”: riparian vegetation, either trees or bushy formations along rivers and streams; 4) “open”: open areas such as crops, meadows and uncultivated land with scattered shrubs, trees or small tree patches; and 5) “urban”: villages. Map accuracy was confirmed in the field.

Estimation of home range

Location data were analysed using the *adehabitat* package (Calenge, 2006) in R (R Core Team, 2019) to estimate the cuckoo home ranges. Only locations recorded more than one hour apart were used in the analyses to ensure time independence. We calculated individual home ranges using 100% minimum convex polygons (100% MCP) and 95% utilisation distribution (95% UD) with

h_{ref} smoothing factor. To examine the effect of the number of locations on home range area independently from the recording order, we used a bootstrap method (1,000 repetitions) to produce an area-locations curve for each individual (incremental area analysis). We used only MCPs for this analysis because utilisation distribution, which use the density of locations to calculate the area, can sometimes decrease in size after adding locations, making the interpretation of the graphical analysis more difficult.

Incremental area analysis is used often to define the minimum number of locations required to identify a home range, i.e. the average number of locations at which the home range area stops increasing despite adding new locations. Because we could not find such a limit (see Results), we used 20 locations per individual as a minimum threshold to calculate home range sizes. We chose that threshold to maximize our sample size while remaining within the range used in studies of other brood parasites (Greater Honeyguide *Indicator indicator*, Spottiswoode *et al.*, 2016 and Common Cuckoo, Nakamura & Miyazawa, 1997). We obtained 20 or more locations from seven individuals in 2009 (four males and three females) and eight individuals in 2010 (five males and three females) for which we estimated 100% MCP and 95% UD. After a preliminary inspection of the data, we tested whether the home range indeed increased with the number of locations significantly faster for females than for males as the graphical results suggested. To do so, we modelled the progressive increments in size of the home ranges in function of the corresponding number of radio-tracked locations with a generalized linear mixed model (GLMM) using the *lme4* package (Bates *et al.*, 2015) in R (R Core Team, 2019). Sex of the home range owner, year and the interaction between number of locations and sex were also fitted as explanatory variables. In the model, which comprised

507 bootstrapped home range values, a random factor was also fitted to account for multiple measures from the same individual.

To control for the different sampling dates and hence, the number of relocations per individual between the two study years, we ran the same analyses (bootstrap and GLMM) with another two different datasets: one including only those relocations of 2010 starting on the same date as in 2009 and another setting the maximum number of relocations per individual to the value obtained in 2009.

Finally, we combined home range data from this study with genetic data obtained during the same period of time (Bolopo *et al.*, 2017) and mapped the nests where we found offspring of the radio-tracked individuals. We found offspring (N = 32) belonging to three radio-tracked females and six radio-tracked males (Supplementary Material,

Appendix 1, Table A2). We obtained the laying range of the females, as minimum convex polygon, and checked for the spatial coincidence with the radio-tracked home range (95% UD). If partial or complete detachment was observed, we considered that the radio-tracked home ranges underestimated the size of the “effective” home range of the cuckoos, defined as the area that fulfils all the nutritional, defensive and reproductive needs of an individual (Burt, 1943).

Habitat use

We examined whether individuals established their home ranges (95% UD) randomly within the study area or favoured certain types of habitat (“second-order selection” *sensu* Johnson, 1980), using a com-

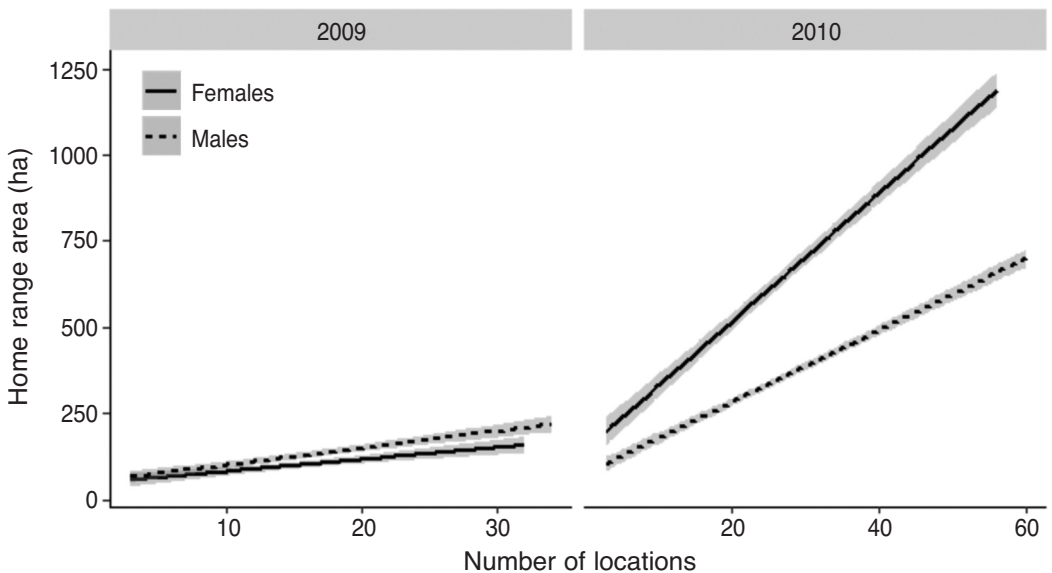


FIG. 1.—GLMM results showing the significant interaction between sex and number of locations on the size of the home range area (100% MCP) of the radio-tracked Great Spotted Cuckoos. Grey area indicates the 95% confidence intervals.

[Resultados del GLMM que muestran una interacción significativa entre el sexo del individuo y el número de localizaciones sobre el tamaño del área de campeo (100% MCP) de los críalos radiomarcados. Las áreas grises indican los intervalos de confianza al 95%.]

positional analysis of habitat use (Aebischer *et al.*, 1993). The analysis was carried out with the *compana* function in the package *adehabitatHS* (Calenge, 2006) in R (R Core Team, 2019). We also used a selection ratio to measure the preference/avoidance for each habitat type: $\text{ratio} = (r - p) / (r + p)$, where r is the proportion of habitat type within the home range and p the proportion of that habitat type available within the study site. Ratio values of +1 indicate maximum selection, -1 maximum avoidance and 0 no preference. Then, we tested the significance of the selection ratio for each habitat type with Wilcoxon signed rank tests. We used the same compositional analysis and selection ratio to study the habitat use by cuckoos within their home ranges (“third-order selection” *sensu* Johnson, 1980). In this case, the selection ratio was calculated with r as the proportion of locations in each habitat type and p as the proportion of each habitat type within the home range.

Home range overlaps and social bonds

We calculated the proportion of home range (95% UD) overlap per dyad of radio-tracked individuals. We divided the overlapping dyads into four groups: females over females (FF), females over males (FM), males over males (MM) and males over females (MF). The overlap values indicate the proportion of the home range of the second individual of the dyad that is overlapped by that of the first individual. For example, in FM dyads the overlap value corresponds to the proportion of the male’s home range that is overlapped by the female’s home range. Therefore, for each dyad we obtained two overlap values, one for the overlap of individual A over individual B, and one for the overlap of individual B over individual A. To address differences in home range overlap between individuals of the same or dif-

ferent sex, we built a linear model using the *lme4* package (Bates *et al.*, 2015) in R (R Core Team, 2019). We set the percentage of overlap as the response variable, and the type of dyad (MM, FF, MF, FM) and year as explanatory variables.

We also recorded the social interactions of the tagged cuckoos. During radio-tracking, upon establishing visual contact with the birds, we noted whether the individual located was alone or accompanied by one or more other individuals. Using the radio-tracking data we analysed the social interactions between individuals that had a chance of interacting with each other, which was set at > 40% of overlap between their home ranges (N = 8 dyads, Supplementary Material, Appendix 1, Table A3). We used the *wildlifeID* package (Long, 2014) in R (R Core Team, 2019) to carry out a dynamic interaction analysis. We used the IAB interaction statistic (Benhamou *et al.*, 2014), which uses both a distance threshold (set at 50m) and a time threshold (set at 3min), to detect interactions (avoidance vs attraction) between the animals.

RESULTS

Estimation of home range

The home range of the radio-tracked individuals varied greatly: 91-1,225ha, 100% MCP, and 167-1,998ha, 95%UD (Supplementary Material, appendix 1, Table A1). We obtained an average of 26 relocations per individual in 2009 (range 21-34) and 44 in 2010 (range 21-60). The increase in home range size (100% MCP) with the number of relocations, proved significantly faster for females than for males (Table 1). Also, home ranges were bigger in 2010 than in 2009, although the tendency was marginally non-significant (Table 1).

To control for the effect of the different length of the sampling period between years,

TABLE 1

Factors affecting the size of the home range (100% MCP) of the Great Spotted Cuckoo. Results of a GLMM, with individual ID set as random factor.

[Factores que afectan al tamaño del área de campeo (100% MCP) de los críalos. Resultados de un GLMM que incluye la identidad de los individuos como factor aleatorio.]

Explanatory variable	Estimate \pm SE	<i>t</i> value	d.f.	P value
Number of relocations	13.925 \pm 0.704	19.77	490	< 0.001
Sex (males)	-4.239 \pm 70.11	-0.060	12	0.953
Year (2010)	131.887 \pm 66.86	1.973	12	0.072
Relocations * Sex (males)	-4.250 \pm 0.90	-4.735	490	< 0.001
N = 507				

we ran two additional models. The first one, which comprised only the locations of the year 2010 obtained from May 3rd (first relocation day in the year 2009) showed qualitatively similar results (Supplementary Material, Appendix 1, Table A4), ruling out an effect of the starting date. In the second model, where we cut the number of locations of the year 2010 to the maximum number sampled in the year 2009 (i.e. 34 locations), the significant interaction between sex and number of locations was also confirmed, and the effect of year became significant, suggesting that home ranges were indeed larger in 2010 than in 2009 (Supplementary Material, Appendix 1, Table A5), as the initial model indicated.

Offspring location and laying ranges

Genetic analysis reported in Bolopo *et al.* (2017) at the same study site, identified 55 adults in 2009 (28 males and 27 females) and 31 adults in 2010 (15 males and 16 females), inferred from the parentage analyses of cuckoo chicks samples (61 chicks sampled in

2009 and 28 in 2010). We found no genetic offspring of three of the captured adults in 2009 (two males and one female) and of another six in 2010 (two males and four females). Pooling all information together, the minimum number of adult cuckoos in the study site was 58 in 2009 and 37 in 2010. The fewer chicks sampled in 2010 were due to lower hatching success of the cuckoo eggs (56% in 2009 and 31% in 2010), which in turn affected the estimation of the number of adults in that year. In fact, cuckoo density most likely increased in 2010, as shown by a higher parasitism rate as compared to 2009 (Baglione *et al.*, 2017). It is important to note here that our radio-tracking data are based on only a fraction of the adult population (maximum 20% in 2009 and 35% in 2010). This is particularly relevant for the interpretation of the home range overlaps described below.

We found between one and nine offspring belonging to nine radio-tracked individuals; six males and three females (see Supplementary Material, Appendix 1, Table A1). Overall, we found that 56.25% of the offspring were raised in host nests within the

home range (95% UD) of their parents, with no significant differences between parental sex (two tailed Fisher exact test: $P = 1$, $n = 32$) or year (two tailed Fisher exact test: $P = 0.490$, $n = 32$). For the offspring outside the home ranges, the average distance \pm 95% CI from the border of the parental home range to the parasitized nest was $1,907 \pm 851$ m (range 200-5400 m, Supplementary Material; Appendix 1, Table A2), with no significant difference between parental sex (two tailed Mann-Whitney test: U-value = 21.5, $P = 0.749$, $N = 32$) or year (two tailed Mann-Whitney test: U-value = 37, $P = 0.795$, $N = 32$). The large proportion of offspring raised outside the radio-tracked home range of females indicates that their “effective” home range, defined as the area that an individual uses to find resources for nutrition, protection and reproduction (Burt, 1943), was in fact larger than that drawn on the bases of radio-tracked movements.

We found that the laying sequences of the three radio-tracked females with known offspring did not follow a consistent sequential pattern, such as laying first within the home range and then outside, or vice versa. Female *cgl11* had all three offspring raised outside her home range; the first egg was laid on March 29th and the last on May 28th. Female *cgl17* had four offspring; the first three eggs were laid inside her home range whereas the last one was outside. Finally, female *cgl9* laid the first egg inside her home range, the next two eggs outside, the fourth egg inside, the fifth outside and the last four eggs inside again. See Supplementary Material, Appendix 1, Table A2 for detailed information on laying dates and distances to the home ranges.

Habitat use

Compositional analysis and Wilcoxon signed rank tests for second-order habitat selection detected significant avoidance of

open areas and preference for pines plantations by the individuals when establishing their home ranges (Table 2), compared to the other habitats available. The compositional analysis for third-order selection detected that Great Spotted Cuckoos significantly preferred to visit areas of riparian vegetation whereas they avoided the urban, forest and open parts of their home ranges, and used pine plantations according to availability (Table 2).

Home range overlaps and social bonds

The radio-tracked home ranges of six dyads overlapped in 2009 as did those of 20 dyads in 2010, indicating that Great Spotted Cuckoos did not defend exclusive territories. Home range overlaps ranged from 0.46% to 100% among dyads, with an average of 27.8%. Average overlap of the different dyad types was: FF dyads 11.0% ($N = 4$, range 1.6-24.9%), FM dyads 33.9% ($N = 16$, range 0.8-100%), MF dyads 27.9% ($N = 16$, range 0.5-84.4) and MM dyads 25.5% ($N = 16$, range 1.1-86.2). There were no statistical differences in overlap between the different types of dyads ($\chi^2 = 1.324$, d.f. = 3, $P = 0.723$), although overlap values were higher in 2009 than 2010 (estimate \pm SE = -25.47 ± 9.62 , $\chi^2 = 7.01$, d.f. = 1, $P = 0.008$).

We found a total of eight dyads whose home range areas overlapped more than 40% (see Supplementary Material, Appendix 1, Table A3 for details). The dynamic interaction analysis showed attraction between individuals for three of the dyads with the time and distance thresholds chosen (Supplementary Material, Appendix 1, Table A3). Dyads formed by male *cgl10* and female *cgl11* and, male *cgl23* and female *cgl24* showed significant attraction values ($P < 0.05$) whereas the dyad male *cgl13* and female *cgl17* only showed a tendency for attraction (Supplementary Material, Appendix 1, Table A3).

TABLE 2

Results of one-sample Wilcoxon signed rank tests for each habitat type to evaluate the significance of the selection ratio for second- and third-order habitat selection of the Great Spotted Cuckoos ($N = 15$). Negative significant estimates indicate avoidance of the habitat type and positive indicate preference. Significant results at $P < 0.05$ in bold.

[Resultados del test de Wilcoxon en cada tipo de hábitat, para evaluar la significación de los análisis de segundo y tercer orden de selección del hábitat de los críalos ($N = 15$). Valores negativos indican evitación, positivos preferencia. Resultados significativos en negrita.]

Analysis	Estimate	95% CI	V-value	d.f.	P
Second-order selection				14	
Pines	0.174	0.104 , 0.249	117		< 0.001
Urban	0.182	-0.078 , 0.423	86		0.151
Riparian	0.157	-0.024 , 0.322	90		0.095
Forest	-0.136	-0.642 , 0.210	49		0.561
Open	-0.052	-0.107 , -0.004	14		0.007
Third-order selection				14	
Riparian	0.806	0.442 , 0.884	105		0.008
Pines	0.314	-0.200 , 0.581	85		0.187
Open	-0.112	-0.187 , -0.015	24		0.041
Forest	-0.782	-0.975 , -0.107	13		0.005
Urban	-0.990	-0.995 , -0.697	2		< 0.001

Three male-female dyads seemed to constitute social pairs. Besides the attraction showed by the dynamic interaction analysis, their home ranges had similar shapes and males' home ranges were always overlapped almost completely by those of the females (99.9%, 99.8% and 100%). The common home range areas of the social pairs were also overlapped by other individuals of the population, both males and females (Figure 2), suggesting a lack of pair exclusive territoriality too. Genetic data showed successful breeding between male *cgl13* and female *cgl17*, with two offspring raised in nests inside their shared home range (Figure 2).

Surprisingly, we also found an extra-pair offspring of male *cgl13* and an extra-pair offspring of female *cgl17* together in a nest outside both individuals' home ranges (Figure 2 empty triangle, Supplementary Material, Appendix 1, Table A1). We found no offspring of the putative pair *cgl10-cgl11*, although we observed them copulating once. Instead, both individuals had descendants with different mates: male *cgl10* within their shared home range, and female *cgl11* outside both of their home ranges (Supplementary Material, Appendix 1, Table A1). No offspring of either individuals *cgl23* and *cgl24* were found.

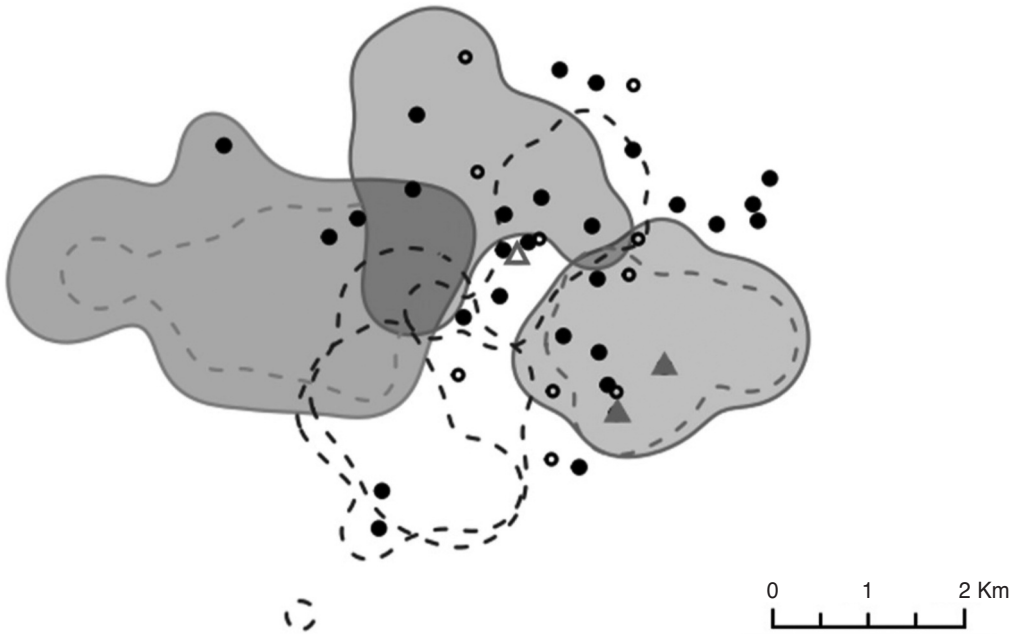


FIG. 2.—Representation of radio-tracked home ranges (95% UD) of the Great Spotted Cuckoo and parasitised host nests. Grey shaded polygons represent female home ranges, dashed lines represent male home ranges. Black dots represent locations of parasitised nests with offspring belonging to adult cuckoos that were not radio-tagged. Open dots represent parasitised nests where genetic samples could not be collected due to hatching failure.

Fully overlapped home ranges, on the left side, represent the social pair *cgl13* (male) – *cgl17* (female). Fully overlapped home ranges, on the right side, represent the social pair *cgl10* (male) – *cgl11* (female). Full triangles represent the location of common offspring of the *cgl10* – *cgl11* social pair. Open triangle represent the locations of two offspring that *cgl10* and *cgl11* obtained with extra-pair mates. [Representación de las áreas de campeo obtenidas con datos de radioseguimiento de los críalos y de las localizaciones de los nidos parasitados. Los polígonos coloreados indican las áreas de campeo de las hembras, las líneas discontinuas las áreas de los machos. Los puntos negros representan los nidos parasitados que contienen pollos de adultos que no fueron radiomarcados. Los círculos indican los nidos parasitados en los que no se pudieron conseguir muestras genéticas debido a fallos en la eclosión de los huevos.

En el lado izquierdo, las dos áreas de campeo totalmente solapadas, pertenecen a la pareja social *cgl13* (macho) – *cgl17* (hembra). Las dos áreas de campeo totalmente solapadas, a la derecha, representan la pareja social 'pair' *cgl10* (macho) – *cgl11* (hembra). Los triángulos rellenos indican los pollos de la pareja *cgl10* – *cgl11*. El triángulo vacío indica pollos que *cgl10* y *cgl11* obtuvieron mediante cópulas extrapareja.]

DISCUSSION

This is the first study, to the best of our knowledge, using concurrent genetic and behavioural data to obtain a comprehensive

view of a brood parasite's mating system. Although the difficulties of data collection inevitably limited our sample sizes, the results shed light on the use of space in the Great Spotted Cuckoo, the socio-ecological

factors that drive it and how these factors ultimately explain the combination of social monogamy and genetic polygamy uncovered in this study population.

From ranging behaviour to mating system

It has been long recognised that the environment affects the mating system of many animal populations by shaping their spatial behaviour (Davies *et al.*, 2012). Such a link has not yet been explored in brood parasites, where the dependence on suitable hosts for reproduction adds further complexity. Theory predicts that a lack of territoriality should increase polygamous mating, by favouring encounters among potential sexual partners (Hauber & Dearborn, 2003). According to this hypothesis, we found that our highly polygamous Great Spotted Cuckoos (Bolopo *et al.*, 2017) did not defend exclusive territories. The radio-tracked home ranges of the tagged individuals overlapped widely but surely underestimated the extent to which cuckoos share the space. Indeed, the genetic data revealed that *i*) we radio-tracked only a fraction of the whole population, *ii*) the “effective” home range of females, i.e. including laying areas, was bigger than their radio-tracked home range and *iii*) several different females laid their eggs inside the radio-tracked home ranges of other females (Figure 2). Therefore, based on complementary genetic and movement data, we define the Great Spotted Cuckoo as non-territorial in this population.

We suggest that a lack of territoriality, and ultimately polygamy, in the Great Spotted Cuckoo depends largely on the ecology of its hosts in the studied area. At Sobarriba, cuckoos mostly moved around riparian vegetation and pine plantations, which are the most productive foraging areas for the species, due to the abundance of caterpillars (pers. observ.), including the cuckoos’ main

prey, the Pine Processionary Moth *Thaumetopoea pityocampa* caterpillars (Valverde, 1953; Mestre Raventos, 1968). These are not, however, the preferred nesting habitats of their hosts (Soler, 1990; Canestrari *et al.*, 2008, Baglione *et al.*, 2016), forcing cuckoos to search for nests away from their feeding areas. The partial detachment between foraging and laying grounds may prevent territoriality, by precluding efficient patrolling and eviction of intruders, as Martínez *et al.* (1998) suggested for a population at Guadix (southern Spain). In addition, the peculiar preference of the Great Spotted Cuckoo for crow nests instead of magpie nests at our study site (Baglione *et al.*, 2017), may constrain territoriality even further. Unlike magpies, which are also common at Sobarriba, crows defend large all-purpose territories and their nests are uniformly dispersed over relatively large areas (Baglione *et al.*, 2005), making their defence unaffordable for the parasite.

Population density

Contrary to expectations, Martínez *et al.* (1998) found that the laying ranges of mainly monogamous females of Great Spotted Cuckoos also overlapped largely in Guadix (Granada, Andalucía, southern Spain). Therefore, although no information is available for males of the Guadix population, it seems that (non) territoriality alone cannot unequivocally predict the genetic mating pattern in this species. Plausibly, the rate of encounter of potential partners might depend also on the population density, as suggested by a previous comparative study that found that the levels of polygamy increased with cuckoo numbers (Bolopo *et al.*, 2017). We therefore suggest that non-territoriality is a “permissive” step towards polygamy, which might arise only when the density of the population reaches a given threshold.

Flexible ranging behaviour?

In this study we have observed that radio-tracked home range size varied annually, being larger in 2010 than in 2009. This could be due to an increase in population density in 2010 (Baglione *et al.*, 2017) that forced cuckoos to use larger areas to find enough host nests. However, given the large geographic variability of host territorial behaviour, which ranges from defence of exclusive territories to semi-coloniality (Birkhead, 1991; Baglione *et al.*, 2005), we might ask whether the Great Spotted Cuckoo goes beyond simple adjustment of home range size and matches the flexibility of its hosts. Intriguingly, in a southern Spanish population in the Sierra Morena, where the cuckoo and its preferred host, the magpie, share foraging grounds and where host nests are especially aggregated compared to other areas (Arias de Reyna, 1998), this brood parasite was reported as territorial. It must be noted, however, that indications of territoriality (Arias de Reyna, 1998 and references therein) were based on data collected from unmarked individuals and should be taken with caution. The extent of plasticity of the territorial behaviour of the Great Spotted Cuckoo and its parallel effect on its mating patterns therefore need further investigation, ideally by applying appropriate standardised methodology (e.g. traceable marked individuals) in multiple populations.

Reconciling social monogamy and genetic polygamy

Specialist brood parasites are expected to rely on female/male cooperation to find a sufficient number of suitable host nests to parasitise (Hauber & Dearborn, 2003). Pair bonding, in addition, should favour parasites that target large hosts that possess defensive adaptations, because the coordinated action

of two partners may increase the chances of laying (Hauber & Dearborn, 2003). Social monogamy would therefore theoretically provide advantages to the Great Spotted Cuckoo, which fulfils the two conditions explained above. Indeed, Arias de Reyna (1998) described a “distraction strategy” in this species, where the male elicits a defensive attack by the magpie hosts, while the female approaches the nest inconspicuously and lays the egg. However, recent video-recorded observations showed that cuckoo females can endure the attack of magpie females inside the nest and manage to lay eggs, without the assistance of a partner (Soler *et al.*, 2014). This shows that intra-pair cooperation in the Great Spotted Cuckoo might be beneficial but is not strictly necessary to parasitise the magpie host. The same situation applies to crows, where females have been observed parasitising nests both alone or in coalition with a mate (DB and VB personal observations). Cuckoos need to find the crow nests unattended to lay their egg, because an incubating crow female, which is double size of the cuckoo, passively protects her clutch very effectively (Canestrari *et al.*, 2009). Crows, unlike magpies, cannot be lured into leaving the nest temporarily because they do not mob the parasite (Soler, 1990), but the coordinated action of a cuckoo pair might increase monitoring of crow nests, improving the chances of laying. The question therefore is, to what extent facultative intra-pair cooperation might select for sexual social bonding in a species where there are counteracting factors that favour polygamy (e.g. lack of territoriality, see above).

Our results show that Great Spotted Cuckoos can form social pairs during breeding season, but relationships are rather loose, and each individual can be solitary a substantial part of the time. Our Great Spotted Cuckoo putative pairs (i.e. pairs of opposite sex that shared a large proportion of their home range) were radio-tracked together

significantly more often than with any other (tagged or untagged) individual. On these occasions, the pairs behaved as such, moving cohesively and coordinately (pers. obs.), and vocalising often. This contrasts sharply with the behaviour of two males that, in spite of sharing a large proportion of their home ranges, were observed together only once. Therefore, after combining genetic and social patterns, the mating system of this species at our study site is better envisioned as loose social monogamy with a high frequency of extra-pair copulations, rather than polygamy.

CONCLUSIONS

The facts that ranging behaviour alone could not predict the genetic mating pattern in the Great Spotted Cuckoo and that, genetic data did not accurately reflect the social interactions between sexes, highlights the need for combining genetic and behavioural information to understand the life history of brood parasites. Our data showed a complex scenario in the Great Spotted Cuckoo, where loose pair bonds can be maintained despite high levels of genetic polygamy and absence of territoriality. However, this might be only one outcome along a gradient of variation of the mating and ranging system caused by factors such as food distribution, host availability and ecology, and the parasite's population density.

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critical review. Daniela Canestrari: Study conception, manuscript critical review. Vittorio Baglione: Study conception, manuscript writing, funding acquisition.

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SUPPLEMENTARY ELECTRONIC MATERIAL

Additional supporting information may be found in the on-line version of this paper. See the volume 67(1) on www.ardeola.org

Table A1. Data from all the captured Great Spotted Cuckoos.

Table A2. Known offspring of the radio-tracked individuals.

Table A3. Description of the data obtained from dyads of individuals whose home ranges overlapped by 40% or more.

Table A4. Factors affecting the home range size of the Great Spotted Cuckoo. Results of a GLMM, individual ID set as random factor. Data including only those relocations of 2010 starting on the same date as in 2009 (ie from May 3rd).

Table A5. Factors affecting the home range size of the Great Spotted Cuckoo. Results of a GLMM, individual ID set as random factor. Data including only the maximum number of relocations per individual obtained in 2009 (ie 34 relocations).

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