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Spatial patterns of egg laying and multiple parasitism in a brood parasite: a non-territorial system in the great spotted cuckoo (*Clamator glandarius*)

Abstract We analysed the spatial and temporal pattern of egg laying in great spotted cuckoo females using microsatellite typing to determine parentage of the eggs and nestlings found in host (magpie) nests. The results showed that there were no exclusive laying territories in the study area. Cases of multiparasitism could be due to single females laying two or more eggs in a nest, or to several females using the same nest. In the latter case multiparasitism was due to a shortage of available host nests. We argue that the need for very large laying areas and the likely small cost of sharing parental care for chicks make the costs of defending territories higher than the benefits, which has constrained the evolution of territoriality in this species.

Key words Brood parasitism · *Clamator glandarius* · Egg laying · Multiple parasitism · Territory

Introduction

Avian brood parasites lay their eggs in the nests of other bird species, the hosts, which raise the parasitic offspring (Payne 1977; Rothstein 1990). The close relationship between hosts and parasites makes this a system especially suitable to study coevolution, due to the (often) drastic reduction of host breeding success produced by parasitism and the dependence of parasites on their host to breed (Rothstein 1990). Studies on brood parasitism have mainly been focused on the effects of parasites on hosts, and the adaptive responses of hosts against parasitism (for example Davies and Brooke 1988; Moksnes

et al. 1990, 1993; Sealy and Neudorf 1995; Sealy 1996; Soler and Møller 1990; Soler et al. 1994). Less is known about behaviour and tactics of parasitism by individual parasites, with some exceptions (Yokel and Rothstein 1991; Jones et al. 1997; Martínez et al. 1998), probably due to the difficulties involved in working with marked birds. In particular, one aspect of the ecology of brood parasitism that deserves more attention is the analysis of the spatial distribution of egg laying by parasitic females, to determine the existence and characteristics of laying territories and the occurrence and extent of multiple parasitism, where several parasitic eggs are found in the same host nest.

In general, it is not clear whether parasites defend exclusive laying territories containing host nests. For example, among cowbirds (*Molothrus* sp.) some studies indicate that females probably defend territories (Rothstein et al. 1984) but others show little evidence for territoriality (Fleischer 1985). Cuckoos in the genera *Cuculus* and *Chrysococcyx* appear to be territorial (Payne 1977; Wyllie 1981), but the information about *Clamator* cuckoos is also contradictory: some studies show evidence for territoriality (Mountfort and Ferguson-Lees 1961; Arias de Reyna et al. 1987) and other studies do not (Gaston 1976). However, all these studies in *Clamator* have been based on egg appearance and/or observations of unmarked individuals.

Multiple parasitism is well documented in several parasitic species (Payne 1977). Multiparasitized nests only occur regularly in parasite-host systems in which the parasitic nestling does not actively kill host eggs or young, but shares the nest with them at least for a certain period of time (Rothstein 1990). This is the case in cowbirds and some cuckoos (*Clamator* sp.; Payne 1977; Rothstein 1990). It is not clear, however, to what extent multiply parasitized nests are the consequence of individual females laying several eggs in the same nest or several females each laying a single egg, or what the relationship is between territoriality and multiparasitism. The studies of this topic have normally been based on egg appearance, with only a few cases in which females were

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identified by molecular methods, which revealed a more or less considerable overlap of the laying areas of parasitic females (Fleischer 1985; Martínez et al. 1998).

Our aims in this study are to determine whether there exist exclusive laying territories in a brood parasitic species, their characteristics, and their relationships with the occurrence of multiple parasitism, as well as to determine the extent of multiparasitism both by the same and by different females. We have studied the great spotted cuckoo (*Clamator glandarius*), for which there is indirect evidence of territorial behaviour (Arias de Reyna et al. 1987), but multiple parasitism is common (Soler et al. 1994). Also, it has been shown using genetic methods that multiple parasitism is due both to the same female laying two or more eggs in a nest and to different females laying in the same nest (Martínez et al. 1998). Two explanations of multiparasitism in great spotted cuckoos in relation to territoriality have been proposed: some authors consider that multiparasitized nests would occur in areas where territories overlap (Arias de Reyna et al. 1982), whereas a high frequency of multiparasitized host nests has been considered in other studies as evidence of non-territoriality (Martínez et al. 1998).

We analysed the spatial and temporal pattern of egg laying by individual great spotted cuckoo females, using genetic methods that allow us to accurately determine which female laid each egg and which male fertilised them. By doing so we will be able to characterise the laying strategies of females and test predictions of several hypotheses regarding territoriality and multiparasitism. However, our conclusions must be restricted to females since we will use the eggs as clues to deduce the behavioural strategy. Due to the absence of direct observations of behaviour, we cannot determine the role played by males in laying strategies or territorial behaviour. Non-monogamous relationships occur in great spotted cuckoos (Martínez et al. 1998, this study), which makes it difficult to extrapolate male behaviour from female behaviour.

We also analyse the spatial and temporal distribution of magpie nests, since great spotted cuckoos depend upon them to breed, and the probability of parasitism is influenced by the pattern of nest availability (Martínez et al. 1996).

Hypotheses and predictions

We have classified the hypotheses about territory and multiparasitism into two different categories: (a) laying strategies with respect to other females/pairs, i.e. territorial hypotheses and (b) laying strategies with respect to the female's own eggs. The hypotheses in categories (a) and (b) are not mutually exclusive.

Territory-based laying strategies

We consider three different hypotheses in which there is a territory exclusively or preferentially used by a female, although with different characteristics.

Hypothesis 1

There is a laying territory exclusively or preferentially used by females, which exclude other females from using it, nests parasitized by two or more females being found only at the boundaries of territories (Fig. 1A). We would expect that, for each female, the mean distance from each nest parasitized by that female to the nearest one parasitized by her (S, Fig. 1A) would be significantly smaller than the mean distance from each nest para-
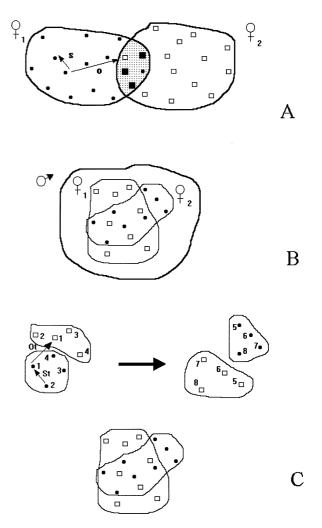

Fig. 1A–C Territorial hypotheses. *Dots* represent nests parasitized by one female and *squares* nests parasitized by another female. *Lines* represent the boundaries of supposed territories. **A** Exclusive territories with overlapping areas (hypothesis 1); *black squares* represent nests parasitized by both females, *S* is the distance from each nest to the nearest one parasitized by the same female and *O* is the distance from each nest to the nearest one parasitized by another female. **B** Females, territories overlap because they are mated with the same male (hypothesis 2). **C** Dynamic exclusive territories (hypothesis 3); *St* is the distance from each egg to the nearest egg (in time and space) from the same female and *Ot* the distance from each egg to the nearest egg (in space) laid at the same time by any other female. *Numbers* by the nests represent laying order. The drawing on the *left* represents the situation early in the season, the drawing on the *right* represents the situation later on and the drawing *below* them shows the pattern of parasitism when time of the season is ignored

sitized by that female to the nearest nest parasitized by another female (O, Fig. 1A).

Hypothesis 2

A female may share territory with another female mated with the same male in a polygynous arrangement, but their territory would not be used by females mated with another male (Fig. 1B). This hypothesis would apply only if polygyny were found to occur. In that case, females sharing territories would be mated with the same male, and for those females the mean distance from each nest parasitized by any of them to the nearest one parasitized by any of them should be significantly smaller than the mean distance from each nest parasitized by any of them to the nearest nest parasitized by a female mated with a different male. Multiply parasitized nests would only contain eggs from females mated with the same male.

Hypothesis 3

If nest availability changes around the area during the season, great spotted cuckoos could follow a dynamic territorial strategy consisting of using small patches with a few active nests. When nests are no longer available in that patch they would move to another area with available nests. In this way, the territory used by two females over the whole season could seem to overlap but females would be exclusively using small areas for short periods of time and then moving to new patches, which could have been used before by another female, where new nests became available (Fig. 1C). We predict that in this case for each female the mean distance from each egg to the nearest egg (in time and space) laid by her (St) should be smaller than the mean distance to the nearest egg (in space) laid the same day by any other female (Ot). Nests parasitized by several females would be the consequence of a shortage of available nests at any time in the season, either of total number of nests available or nests not parasitized yet (nest availability is negatively related to number of cuckoo eggs per magpie nest; Martínez et al. 1996).

Strategies affecting a female's own eggs

These hypotheses try to explain the pattern of egg dispersion by individual females among host nests and the multiple parasitism of host nests by a single female as a function of nest availability.

Hypothesis 4

Females lay their eggs close to each other, i.e. in nests situated in the surroundings of the nests where the pre-ceding eggs were laid. If this is the case we predict that eggs will be laid closer to each other than expected as a function of nest availability, and then the mean distance from the nest where an egg was laid to the nest where the following egg was laid (F) should be smaller than the mean distance from the first nest to all the other nests available in the area (A).

Hypothesis 5

A possible strategy could be to lay a single egg per nest. This hypothesis predicts that multiple parasitism is always due to several females laying in the same nest.

Hypothesis 6

Another strategy would be to lay a single egg per nest except when there are no other nests available, in which case the nests would be used twice or more. In this case the probability of finding an egg in a nest along with eggs from the same female would be negatively related to nest availability.

Methods

Study area and field work

Field work was carried out in 1997 in the Hoya de Guadix (Granada, Southern Spain). This is a patchy area, with sparse vegetation and treeless areas alternating with discontinuously distributed almond (*Prunus dulcis*) groves. The almond groves are the nesting site of magpies (*Pica pica*), the main European host of great spotted cuckoos (Cramp 1985). We worked in a discrete patch of around 1.75 km^2 within our main study area, near the village of Ferreira (UTM 30S 0496 4114), consisting mainly of almond groves and surrounded by two hills with pines (*Pinus halepensis*). Further information on magpie-great spotted cuckoo interactions can be found elsewhere (Soler et al. 1994, 1997, 1998).

Adult great spotted cuckoos were caught using mist nets throughout the breeding season, setting up the nets in adequate places such as feeding or resting areas. Birds were marked with a metal ring (Spanish Institute for Nature Conservation, ICONA) and an unique combination of colour rings on both tarsi. Approximately 200 µl of blood was extracted from the brachial vein and stored in 1 ml of 100% ethanol in a microfuge tube.

During the breeding season we searched for magpie nests. Once found, they were checked periodically in order to detect parasitism cases and to record reproductive parameters such as laying date, clutch size, hatching date, etc. Laying date of cuckoo eggs was accurately determined only in 20 of the 43 eggs laid, and for the rest we estimated it as 14 days (incubation period) before hatching, which was determined with an error of 1 day. Because great spotted cuckoos lay most of their eggs in the middle of the magpie laying period (71.3% of the eggs; Soler et al. 1997), they are incubated as soon as or shortly after they have been laid. The estimate of laying date from hatching date should therefore have a small error. Cuckoo chicks were ringed when 15 days old and we obtained blood samples from them. We collected all but three unhatched eggs. No chick died before being sampled and only one nest was predated, resulting in 36 samples (33 blood samples from chicks and three samples from unhatched eggs), the 83.7% of total eggs laid in the plot.

Magpie nests were located using a detailed map (1:25000) of the area and distances between them were measured on the map. Because seven is the modal magpie clutch size in our study area, and most cuckoo eggs are laid during the magpie laying period (Soler et al. 1997), we considered each nest as available to be parasitized by cuckoos during a period of 7 days from the day magpies laid the first egg. We estimated nest availability in a given day as the number of nests available in the area.

Laboratory work

DNA was extracted using standard protocols from blood samples and then used to carry out parentage analyses with the nestlings/eggs sampled. Parentage assignment was carried out by microsatellite genotyping, as previously reported in Martínez et al. (1998). Microsatellites are loci characterised by a high variability, mendelian inheritance and codominance, particularly well suited for individual identification and parentage analyses (Bruford and Wayne 1993). More details about the microsatellite loci and genotyping procedures can be found in Martínez et al. (1998). We also sexed adult great spotted cuckoos using molecular methods, since sexes are morphologically similar in this species (Cramp 1985). Sexing was carried out using a combination of sex-specific PCR primers and single-strand conformation polymorphism analyses as described in Martínez et al. (1998).

Parentage determination

Every individual was genotyped for six polymorphic loci (Cgl 1, Cgl 2, Cgl 3, Cgl 4, Cgl 5 and Cgl 6; Martínez et al. 1998). The probability of identity, i.e., that two individuals had the same genotype, was 2.4×10^{-5}, and the probability of false parental inclusion, i.e. the probability of failing to detect an individual incorrectly assigned as a parent, was 3×10^{-3} (for details of calculations see Martínez et al. 1998).

The genotypes of adult birds were compared with those of the nestlings. We considered an adult bird to be the possible parent of a chick when its genotype was compatible with that of the chick, that is, when it could have contributed either allele at every locus in the nestling's genotype. After all potential parents had been identified, we investigated which pair of male and female individuals could have donated the allele combination to the chick, and that pair was considered to be the parents of that particular chick (Martínez et al. 1998). We assigned 27 chicks to only one male and one female, that were considered to be their parents, and 9 chicks to only one individual, two females and a male (Table 1). For these 9 individuals we deduced the putative genotype of the missing father/mother, by comparing the genotypes of the known parent and each individual, and gave it a specific name (II, III and IV, Table 1). We then compared the deduced genotypes with the genotypes of all the chicks sampled and checked that none of the three missing adults could be the father/mother of any other chick but the ones considered in Table 1.

Statistics

We followed Sokal and Rohlf (1995) and Siegel and Castellan (1988). The values given are means and standard deviations (SD). All tests are two-tailed. To test the effect of nest availability on the probability that an egg is (a) found in a nest along with eggs from other females or (b) found in a nest parasitized twice or more by a single female, we performed logistic regressions with two different dependent variables. When testing (a) the dependent variable was coded 0 for eggs found in nests parasitized only by one female and 1 for those in nests parasitized by several females. When testing (b) the dependent variable was coded 0 for eggs in nests parasitized once by a female and 1 for eggs found in nests parasitized twice or more by the same female. A logistic model was fitted using the maximum-likelihood method (Sokal and Rohlf 1995). The deviance

($2 \times$ log-likelihood) for this model was calculated. We examined the effects of omitting each of the independent variables by fitting the model without that variable and then considering the difference in deviance between models including and excluding the variable being tested. The final model was identified when the omission of any variable would have caused a significant increase in the deviance. As independent variables we used nest availability the day the egg was laid, both total nest availability and the availability of nests not yet parasitized.

Results

Spatial and temporal distribution of magpie nests

Nearest nest distance ranged between 50 and 420 m with a mean value of 140 m (SD = 90). The distribution of nearest nest distances was significantly different from a Poisson distribution ($\chi^2 = 65.7$, $P < 0.0001$), more nests than expected being at a distance of 50–150 m. This indicates that nests were not randomly distributed but regularly spaced, probably as a consequence of the territorial behaviour of magpies (Birkhead 1991).

Nests were not, however, regularly distributed in time, because egg laying peaks at the beginning of the season and then the number of active (in egg laying) nests decreases gradually until the end of the season (Fig. 2A). Therefore, nests are for cuckoos a resource
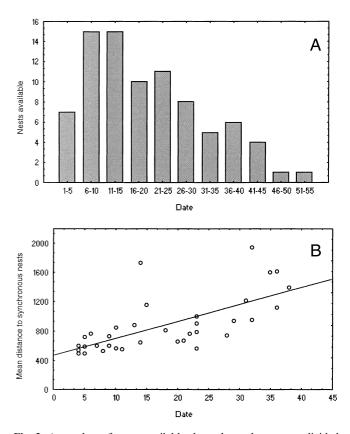

Fig. 2 A number of nests available throughout the season, divided into 5-day periods. **B** Relationship between the date of the first magpie egg in a nest and the mean distance from that nest to all the other simultaneously available

for which availability changes with time in the season, since, in order to be successful, cuckoos must lay their eggs during the few days of the magpie egg-laying period (Soler et al. 1997). In our study area the number of nests simultaneously available to be parasitized significantly decreased with the laying date of cuckoo eggs ($r = -0.83$, $P < 0.0001$, $n = 35$). As a consequence of the fall in number of available magpie nests with date, the mean distance between simultaneously available nests increased with the laying date of the nest ($r = 0.68$, $P < 0.0001$, $n = 37$). Thus, even though nests are regularly spaced, available nests are closer to each other at the beginning than in the middle or at the end of the season (Fig. 2B).

Parentage analyses and frequency of multiple parasitism

We identified four different females laying in the area; three of them were captured but we missed the last one, which laid the fewest eggs (Table 1). Females C9709, C9712 and C9715 had their eggs fertilized by two different males each, and all males sired offspring from only one of the females in the study area. Thus their mating could be monogamous with extra-pair fertilizations in the females, polyandrous or promiscuous, but found no evidence of polygyny in the area. Females laid a high number of eggs, except C97IV, and used between 3 and 11 nests (Table 1).

There were 14 multiply parasitized nests out of a total of 24 parasitized nests (58.3%), a percentage similar to those reported before (Soler et al. 1994; Martínez et al. 1998), but we were able to determine parentage for all eggs in only 10 nests (we missed 1 predated nest and in 3 cases we could not sample one of the eggs). Out of these ten nests, four (40%) had eggs from more than one female and six (60%) were cases of multiple parasitism by single females. There was variation in the degree in which females used nests twice or more (MS, Table 1),

or used nests also parasitized by other females (MO, Table 1).

Territorial hypotheses: are females territorial?

Figure 3 shows the distribution of nests parasitized by each female. The laying range was approximately 1.60 km² (C9709), 0.45 km² (C9712), 1.45 km² (C9715) and 0.80 km² (C97IV). Laying areas overlapped widely, invalidating hypothesis 1: for female C9715 there were no significant differences between S and O (Table 2; Wilcoxon matched pair test, $z = 1.60$, $P = 0.11$, $n = 8$). For C9709 and C9712 the differences were significant, but S was higher than O (Table 2; $z = 2.49$, $P = 0.01$, $n = 11$ and $z = 2.20$, $P = 0.03$, $n = 6$, respectively), which is contrary to the prediction of exclusive laying territories. The small sample size for C97IV ($n = 3$) does not allow a statistical comparison, but S was also higher than O (Table 2).

With respect to the second hypothesis, the mating system does not account for the wide overlap of laying territories, because polygyny was not found to occur and two females parasitizing the same nest(s) were never mated with the same male.

Regarding hypothesis 3, St is not significantly different to Ot for any of the females (Table 2; Wilcoxon matched pair test: C9709, $z = 0.98$, $P = 0.33$, $n = 12$; C9712, $z = 0.52$, $P = 0.60$, $n = 6$; C9715, $z = 0.86$, $P = 0.39$, $n = 12$). Again the small sample size for C97IV ($n = 3$) does not allow statistical comparisons, but St was higher than Ot, which is contrary to the predictions. These analyses could be obscured by the effect of nest availability, if females only have territories when nest availability is high, but not when nest availability is low. We calculated St and Ot for each female when nest availability is high (five or more; five is the mean number of nests available in the days when cuckoo eggs were laid) and low (four or less nest available). The results are shown in Fig. 4. No comparison was significant. Therefore our data do not support any of the territorial hypotheses, and we conclude that there are no exclusive laying territories in great spotted cuckoos.
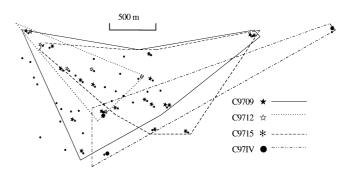
Table 1 Parentage assignment of the eggs/nestlings sampled in the study. For each female, which male fertilized the eggs, how many eggs, how many nests were used to lay them, the percentage of those nests used twice or more by the same female (*MS*) and the percentage of those nests parasitized by other females too (*MO*) is specified. Parentheses indicate those chicks that were assigned to only one of the adults captured and for which we deduced the genotype of the missing father/mother, marked with an *asterisk*

Female	Mate	Number of eggs/nestlings	Number of nests used	MS	MO
C9709	C9708	7	11	9.1%	36.4%
	C9710	5			
C9712	C9713	6	6	33.3%	33.3%
	C97II*	(2)			
C9715	C9711	9	8	50.0%	25.0%
	C97III*	(3)			
C97IV*	C9714	(4)	3	33.3%	33.3%

Fig. 3 Location of nests parasitized by each of the four females. Each female is represented by a different *symbol* and her laying range with a different *line style*

Table 2 Estimates of territoriality for the great spotted cuckoo females in the study (*S* the mean distance from each nest parasitized by one female to the nearest nest parasitized by her, *O* the mean distance from each nest parasitized by one female to the nearest nest parasitized by another female, *St* the mean distance from each egg to the nearest egg (in time and space) laid by the same female, *Ot* the mean distance from each egg to the nearest egg (in space) laid the same day by any other female). The *P* value corresponds to the comparison of S with O and St with Ot using a Wilcoxon matched pair test (see Results). The mean values for C97IV were not statistically compared due to small sample size

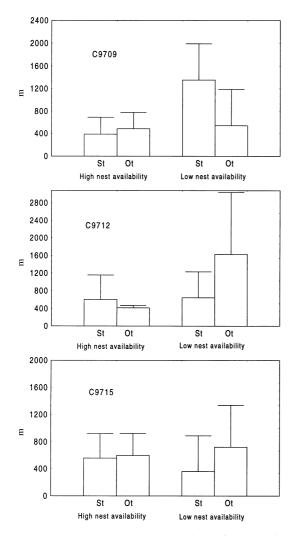|	S	O	P	St	Ot	P
C9709	334.5 (291.4)	108.2 (112.5)	0.01	869.1 (694.4)	511.6 (479.4)	0.33
C9712	306.7 (114.1)	78.3 (75.2)	0.03	626.6 (506.7)	1021.6 (1110.9)	0.60
C9715	371.3 (312.8)	166.3 (125.9)	0.11	459.2 (443.7)	660.0 (474.1)	0.39
C97IV	264.0 (227.3)	220.0 (210.7)		1680.0 (1122.2)	1082.5 (763.7)	

Fig. 4 *St* and *Ot* values (see legend to Fig. 1) for both high nest availability (five nests or more) and low nest availability (four nests or fewer). *Bars* are mean values and *whiskers* SDs

Fig. 5 Values of the distance from the nest where an egg was laid to the nest where the following egg was laid (*F*) and the distance from the nest where an egg was laid to all the other nests available in the area (*A*) for each of the four females. *Bars* are means and *whiskers* SDs. Significance level of the Wilcoxon matched-pair test and sample size are also shown, except for the last female where sample size was too small to allow statistical comparison

Pattern of egg dispersion by individual females

The data do not support hypothesis 4, i.e. that females lay their eggs in those nests situated in the surroundings of the nest where the preceding egg was laid. The distance from the nest where an egg was laid to the nest where the following egg was laid (F) was not significantly different from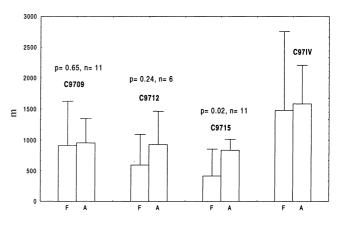 the mean distance from the first nest to all the other nests available in the area (A) for C9709 and C9712. They were very similar for C97IV, and F was significantly smaller than A for female C9715 (Fig. 5). However, this is because this female used half of the nests twice (F = 0, Table 1). When ignoring those cases of consecutive parasitism in the same nest, F and A were not significantly different for C9715 either (Wilcoxon matched pair test, $z = 1.35$, $P = 0.17$, $n = 7$).

We also investigated, for each pair of consecutive eggs laid in different nests, the rank of the second nest in the list of nests synchronous to the first one and sorted by distances to it (the nearest having rank 1, the second 2 and so on). We found that cuckoos did not use nests near to the one previously parasitized (mean rank used $= 6.8$ SD $= 3.67$). Dividing the rank of the nest used by the number of nests available gives an index that varies from 0 (the nearest one) to 1 (the farthest one), whose mean value is 0.59 (0.22). This value does not differ among the three females for which we have data (Kruskal-Wallis test $H_{2,18} = 2.54$, $P = 0.28$).

Nest availability conditions the pattern of egg dispersion within the breeding area. The distance from each egg to the preceding egg laid by the same female increased with laying date ($r = 0.41$, $P = 0.02$, $n = 31$), as did the distance between synchronous nests (Fig. 2B).

Thus, because nests available at the beginning of the season are closer to each other than nests available at the end of the season, those eggs laid at the beginning of the season are closer to each other than eggs laid at the end of the season. A multiple regression model with distance to the preceding egg as dependent variable and laying date and mean distance from the nest where the egg was laid to all synchronous nests as independent variables resulted significant (multiple $R = 0.45$, $P = 0.05$, $n = 28$). The effect of laying date became non significant (partial $r = -0.22$, $P = 0.42$) whereas the effect of mean distance to synchronous nests was significant (partial $r = 0.59$, $P = 0.03$).

Multiple parasitism of host nests

Nest availability had a significant effect on the probability that eggs of different females are found in a nest (Table 3, final model $\chi^2 = 14.5$, $df = 1$, $P = 0.0002$). Indeed, nests parasitized by single females were synchronous with a mean of 14.4 (4.3) nests, whereas nests with eggs of several females were in synchrony with only 7.25 (4.3) nests, the differences being significant (Mann-Whitney U-test, $z = 2.35$, $P = 0.02$, $n_1 = 17$, $n_2 = 4$).

With respect to multiparasitism by single females, hypothesis 5 is not supported by our data. No female laid all her eggs in different nests (Table 1), though female C9709 used twice only one of the nests. This and the data from our previous work (Martínez et al. 1998) that revealed more cases of multiparasitism due to single females, seem to indicate that females are flexible in the decision of using once or more a particular nest. However, none of the two variables considered (Table 3) had a significant effect on the probability of an egg being found in a nest along with eggs from the same female ($\chi^2 = 0.35$, $df = 2$, $P = 0.84$). This also invalidates hypothesis 6 and suggests that laying twice or more in the same magpie nest is in general independent of the availability of nests. Accordingly, there were no differences in the number of nests in synchrony with nests parasitized once by single females and those in synchrony with nests parasitized twice by the same female:

Table 3 Maximum likelihood estimates of the slope parameters (S) and their probabilities (P) of logistic models considering the effects of all the independent variables on **a** the probability of finding an egg in a nest with eggs from other females, and **b** the probability of finding an egg in a nest along with eggs from the same female. Differences between deviances D for models with and without each variable and their probabilities P are also presented in the first analysis (*NA* total nest availability, *UNA* availability of unparasitized nests)

	a				b	
	S	P	D	P	S	P
NA	−0.95	0.04	6.21	0.01	0.02	0.99
UNA	0.46	0.28	1.23	0.26	−0.06	0.81

14.3 (4.3) and 14.6 (4.7) respectively (Mann-Whitney U-test, $z = 0.04$, $P = 0.96$, $n_1 = 10$, $n_2 = 7$).

Discussion

Non-territorial system in great spotted cuckoos

Territories can be defined as more or less exclusive areas defended by some individuals (Davies and Houston 1984), whose aim is to get control over resources such as nesting areas, food supplies or mates, especially during the breeding season (Lack 1968; Gill 1990; Møller 1990). There are two major aspects of territorial behaviour: the active defence of territories against rivals for at least some period of time, and the primary, if not exclusive, use of the territory by the defending individual, its mate and progeny (Gill 1990).

There are practical problems in characterizing territorial defence and individual interactions in parasitic species because their inconspicuous behaviour makes them very difficult to observe, particularly in the case of the secretive cuckoos. However, the second aspect of territoriality, exclusivity in the use of the breeding area, may be indirectly estimated in brood parasites by the pattern of use of resources, in this case host nests, which it is now possible to determine using molecular methods. It is for this reason that we deal with territoriality from the perspective of exclusivity of use in this study. If we assume that territorial females (pairs) exclude other females from the area where they are laying, even though we do not know whether the males, the pair or only the females defend the territory, then great spotted cuckoos in our population are non-territorial, i.e. females or pairs do not maintain exclusivity over the laying areas and follow a non-territorial egg laying strategy.

Territorial behaviour incurs costs, such as time and energy spent in patrolling territory boundaries, as well as benefits, like monopolising resources and obtaining higher reproductive success (Davies and Houston 1984). It has long been accepted that we would only expect an animal to spend time and energy maintaining a territory when the difference between benefits and costs is apprecicable (concept of economic defendability, Brown 1964). Three main factors affect the economic defendability of resources: quality and distribution in space, temporal distribution and competition for resources. If the cost of defending an area increases with territory size, because more intruders will come into the area and the owner will have to patrol longer distances, there will be an optimal territory size for economic defence, influenced by changes in resource quality and competitor density (Davies and Houston 1984). Moreover, it has been argued that very high defence costs may lead to increased territory overlap or absence of territorial defence in some species (Stamps and Buechner 1985).

Great spotted cuckoos would benefit from a large territory by monopolising a large number of host nests. However, the size of a territory containing the number

of nests necessary for them to breed might be too large to be economically defendable, or, in other words, the optimal territory size for economic defence could be too small to contain the adequate number of nests. The evidence available shows that great spotted cuckoos need large areas to lay all their eggs (this study; 9 km^2, Mountfort and Ferguson-Lees 1961; 2.5 km^2, Mundy and Cook 1977; 3.7 km^2, Arias de Reyna et al. 1987), probably too large to be defended efficiently against intruders.

The reason for these large breeding areas is the dispersion of magpie nests and their quality as resource. Great spotted cuckoos select the best quality magpie pairs among those available for parasitizing (J. Soler et al. 1995); this probably explains why they do not parasitize neighbouring nests sequentially but move around the area and choose nests that are not necessarily those nearest to the last one parasitized. This makes the real area used for laying a certain number of eggs larger than the expected area containing only the nests needed for that number of eggs.

It is, on the other hand, unnecessary to maintain such a large area throughout the season, since nests become unavailable to be parasitized after magpies finish laying. Another possibility would be a dynamic territorial system (hypothesis 3), where the exclusive laying areas are small, economically defendable patches in different places within the main area at different moments in the season as a function of nest availability (Fig. 1C), but our data do not support this hypothesis either. As a consequence of both cuckoo nest selection and heterogeneity in the temporal distribution of nests, it becomes impossible to maintain small, defendable areas, since cuckoos must search for nests over an increasingly larger area in the course of the season as inter-nest distances increase with time.

There is another reason that makes territory defence unlikely. Great spotted cuckoos feed on caterpillars, which are normally concentrated in small patches within the breeding area, most commonly in the pines surrounding the main magpie nesting area. Cuckoos must spend an apprciable proportion of their time budget feeding outside the nesting area (personal observation) and this probably makes it very difficult for them to chase intruders away efficiently.

Costs and benefits of multiparasitism

Our results suggest that multiparasitism is a consequence of both a non-territorial system and cuckoo nest selection. Nests parasitized by two females tend to occur when nest availability is low, whereas the occurrence of nests parasitized by single females are independent of nest availability and these nests are probably used twice or more because they are in some way preferred by adult cuckoos to other available nests. J. Soler et al. (1995) showed that great spotted cuckoos select the bigger nests of magpies of higher parental quality, and it could be that nests parasitized twice by a female are better quality nests. Unfortunately we could not measure the nests and we cannot test this hypothesis.

As argued above, the evolution of territories can be considered using a cost-benefit approach. With a non-territorial system, cuckoos run the risk that a percentage of their offspring will be raised together with other cuckoo nestlings in multiparasitized nests, but what are the costs of multiparasitism to cuckoo chicks? Theoretical costs of multiple parasitism are different for different parasitic species. In species such as the common cuckoo (*Cuculus canorus*) females must ensure that only one parasitic egg is laid in each nest because the parasitic nestling will eject the rest of the eggs in the nest shortly after hatching, a likely cause of the evolution of territoriality in this species (Wyllie 1981). However, those species whose chicks do not evict host offspring, like cowbirds and great spotted cuckoos, may use the same nests twice or more provided that hosts are able to successfully rear several parasitic chicks, as happens in the magpie-great spotted cuckoo system (Soler et al. 1998). The fact that great spotted cuckoo females sometimes lay two or more eggs in the same nest despite the availability of alternative nests is an evidence that sharing host parental care might be not so costly. Soler et al. (1998) have shown that breeding success of cuckoos is not significantly different in magpie nests with one, two, three or four cuckoo chicks, decreasing significantly from five chicks onwards. All nestlings in multiparasitized nests in this study fledged successfully. Providing that multiparasitized nests do not contain more chicks than hosts are able to rear, costs of multiparasitism could be lower than the costs of defending large laying territories or even of defending small territories with an inadequate number of host nests. If that was the case, territorial mechanisms would not be of selective value.

Moreover, multiple parasitism in the great spotted cuckoo might have benefits for the chicks once they leave the nest. Great spotted cuckoo fledglings join together in small flocks communally attended by groups of magpies (M. Soler et al. 1995). Birds in flocks receive more food from magpies than solitary birds (M. Soler et al. 1995). If sharing the nest with other chick(s) increases the probability of joining a flock after fledging, then the cost of sharing parental care in the nest might be compensated by the benefits of joining flocks. These benefits may not only be related to receiving better parental care by magpies but also to the process of learning to recognize their own species (M. Soler and J.J. Soler, unpublished work).

Patterns of egg laying in other brood parasites

As mentioned in the Introduction, few studies have addressed the issue of territoriality in brood parasites with an accurate knowledge of the identity of laying females. Nonetheless, the system seems to be similar in cowbirds, where ranges of females overlap extensively, both in

brown-headed cowbirds *Molothrus ater* (Fleischer 1985; Rothstein et al. 1986) and in shiny cowbirds *M. bonariensis* (Kattan 1997). Shiny cowbirds females seem to parasitize host nests randomly, and do not show territorial defence (Katttan 1997; Lyon 1997). Lyon (1997), using egg morphs and visual comparison of spotting patterns, concludes that shiny cowbird females lay a single egg per nest, and argues that multiple parasitism is a consequence of a random laying strategy combined with a high parasitism rate. The same has been suggested for the brown-headed cowbird (Orians et al. 1989).

The evolution of territoriality is unlikely in high-fecundity, generalist brood parasites, such as shiny cowbirds, that follow the "shotgun" strategy of brood parasitism, whose success seems to rely more in a high fecundity than in a careful selection of host nests (Kattan 1997). Although great spotted cuckoos are not generalists to the same degree as cowbirds and seem to select which nests they parasitize, the possibility that several nestlings can be reared in a host nest may reduce the cost of non-territoriality and multiparasitism.

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