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THE EFFECT OF MAGPIE BREEDING DENSITY AND SYNCHRONY ON BROOD PARASITISM BY GREAT SPOTTED CUCKOOS[1]

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Abstract. Nesting density and synchrony by hosts may indirectly serve as a defense mechanism against brood parasites. Here we examine the relationships between spatial and temporal distribution of host nests and the probability of being parasitized. We use as host species the Black-billed Magpie (*Pica pica*), a species that is parasitized by the Great Spotted Cuckoo (*Clamator glandarius*) in southern Europe. We also examined the differences in parasitism rate in nearby plots that differ in magpie social organisation. Results show that increased proximity to other nests and specially laying synchrony both reduced the probability of being parasitized. Consequently, magpies breeding synchronously in dense plots may experience an indirect advantage against brood parasitism with respect to low density, low synchrony plots.

Key words: Parasitism rate; synchrony; density; Clamator glandarius; Pica pica.

INTRODUCTION

Avian brood parasites lay their eggs in the nests of hosts that take care of the parasitic offspring from incubation to independence. This adversely affects host fitness in ways that vary in different parasite-host systems (Rothstein 1990). The rate of parasitism in particular host species may be influenced by various behavioral, historical and ecological factors such as the ability of hosts to recognize and reject parasitic eggs (Davies and Brooke 1989), the time of duration of sympatry between hosts and parasites (Briskie et al. 1992, Soler and Møller 1990) and the suitability of the host's diet to parasitic chicks (Mason 1986).

One of the ecological factors that may influence the rate of parasitism is the dispersion pattern and social organization of host species. For example, it has been argued that hosts might avoid parasitism by nesting in close aggregations (Rothstein 1990). The mechanisms proposed for this effect are a more successful nest defense in high density plots through group defense (Freeman et al. 1990), or the inability of the parasite to parasitize a large number of synchronous nests ("swamping effect," Robertson 1973, Clark and Robertson 1979). Conversely, brood parasitism, as a special kind of predation, may influence the nest distribution of host species (Clark and Robertson 1979).

The Black-billed Magpie (*Pica pica*) is a corvid that occurs throughout the Palearctic region and shows a remarkable variability in nest-spacing patterns. Magpies are territorial, but the nature of their territories differs between populations (Birkhead 1991). Northern European magpies defend relatively large all-purpose territories, about five ha, nesting normally at low densities (Vines 1981, Baeyens 1981, Birkhead 1991), whereas magpies in North America defend very small territories around the nest, nesting at high densities and in aggregations (Reese and Kadlec 1985, Birkhead 1991, Dhindsa and Boag 1992). Data from South Spain and North Africa show that breeding density is notably high and that the spatial distribution is clumped (Arias de Reyna et al. 1984, Birkhead 1991, Redondo and Castro 1992), similar to the spatial organization of American magpies. Differences between northern and southern European magpies may be explained by ecological conditions, such as nest-site availability and food abundance (Birkhead 1991). However, brood parasitism may also be important.

The Great Spotted Cuckoo (*Clamator glandarius*) is a partially migratory parasitic member of the family Cuculidae, with some individuals resident in Africa and others moving to southern

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Europe to breed (Cramp 1985). In Europe, its main host is the magpie (Cramp 1985). As a rule, cuckoo chicks hatch several days before magpie chicks, which results in the magpie chicks starving, losing in competition with the larger, heavier cuckoo chicks (Soler 1990, Soler and Soler 1991). Therefore, parasitism strongly decreases the reproductive performance of magpies, since in most of the parasitized nests only the cuckoo(s) fledge (Soler et al., in press).

Different south European magpie populations have been exposed to brood parasitism by the Great Spotted Cuckoo for a variable time. Magpie social organization could be influenced by parasitism if the probability of being parasitized varied with differences in spatial and temporal organization of magpie populations, and different parasitism rates could be in part due to different spatial and temporal magpie organization patterns. In this study we analyze whether spatial or temporal proximity to other nests affects the probability of a magpie nest being parasitized.

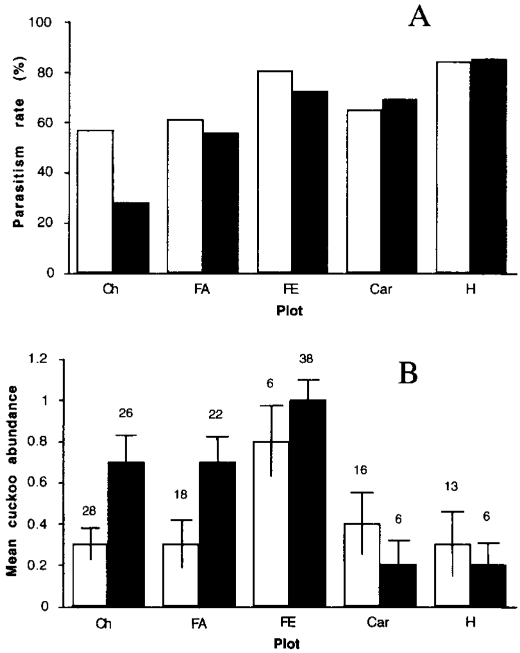

FIGURE 1. Parasitism rate in the five study plots both years of study (A) and mean estimate of cuckoo abundance (birds/hour) for each study plot (B). White bars represent 1992 values and black bars represent 1993 values. Horizontal lines are standard errors, and numbers above the bars are sample sizes. Sites are as follow: Ch, La Calahorra; FA, Fuente Alamo; FE, Ferreira; Car, Carretera; H, Hueneja.

STUDY AREA AND METHODS

We studied magpie-cuckoo interactions in the Hoya de Guadix, near Granada in southern Spain. The Hoya de Guadix is a high-plateau with a semi-arid climate. Vegetation is sparse and the habitat patchy; treeless areas alternate with almond (*Prunus dulcis*) plantations and holm oak (*Quercus rotundifolia*) patches. Magpies nest preferentially in the almond fields. We studied several plots of different size separated by treeless fields, namely La Calahorra (3.01 km^2), Fuente Alamo (0.82 km^2), Ferreira (1.16 km^2), Carretera (3.3 km^2) and Hueneja (4.15 km^2). The distance between plots ranges from four to 15 km.

Field work was carried out during the spring of 1992 and 1993. We found 131 nests in 1992 and 157 in 1993, 87 and 88 of which (66.4% and 56.1%, respectively) had been parasitized. The parasitism rate in the five plots varied between 28% and 86% (Fig. 1A). We located first nests on aerial photographs to calculate nearest neighbor distances and magpie nest density. Nests were checked at least once a week, and reproductive parameters such as first egg date, clutch size, number of chicks hatched, and number of chicks fledged were recorded for most of the nests. Breeding success was calculated as the ratio between chicks fledged and eggs laid. We considered a nest as parasitized if it contained one or more cuckoo eggs.

During the field work, we recorded the number of cuckoos seen in each plot, specifying whether they were chased by magpies, and how many birds chased them. We used the mean number of cuckoos seen per hour while checking nests as an estimate of cuckoo abundance. This method resembles line transects, which are known to give a relative estimate of bird abundance (Järvinen and Väisänen 1975).

MEASURING SPATIAL AND TEMPORAL PROXIMITY

As an index of spatial proximity to other magpie pairs, or density index, we quantified the number of pairs in a 250 meter-diameter circle around the focal nest. To measure the degree of synchrony of each nest, we used the number of temporal neighbors (Westneat 1992), a variable that measures, for each nest, the number of pairs in the same plot starting to lay within three days of the focal nest. This variable is adequate to test the effect of synchrony on parasitism probability

TABLE 1. Maximum likelihood estimates of the slope parameters (S) and their probabilities (*P*) of logistic models for 1992 and 1993 considering the effects of all the variables in parasitism rate. Differences between deviances (D) for models with and without each variable and their probabilities (*P*) are also presented.

	All the variables in the model				Final model	
	S	*P*	D	*P*	S	*P*
1992						
Cuckoo density	1.33	0.31	1.22	0.28		
Laying date	0.03	0.22	1.69	0.19		
Temporal neighbors	−0.09	0.006	8.24	0.004	−0.11	0.002
Density index	−0.14	0.41	0.82	0.36		
1993						
Cuckoo density	1.14	0.16	2.03	0.15		
Laying date	−0.003	0.84	0.04	0.85		
Temporal neighbors	−0.16	0.0004	15.33	0.0009	−0.14	0.0007
Density index	−0.61	0.0007	13.68	0.0002	−0.50	0.001

because it gives a quantitative measure of the number of nests in each plot that are at a similar breeding stage, and thus the number of nests that are simultaneously available to the parasite.

STATISTICAL PROCEDURES

Statistics follow Sokal and Rohlf (1995) and Everitt (1992). A logistic regression was used to analyze whether spatial proximity and temporal synchrony have any effect on the probability of being parasitized. A logistic model was fitted using the maximum-likelihood method and the deviance (2·log-likelihood) calculated. We examined the effects of omitting each of the 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 caused a significant increase in the deviance.

We performed a logistic regression for both years separately with the status of parasitism as dependent variable and four independent variables: plot cuckoo density, laying date, number of temporal neighbors and density index. Using plot cuckoo density as independent variable permitted us to control for potential effects of different cuckoo densities in the plots even though estimates of cuckoo abundance (Fig. 1B) were not different between plots in 1992 (ANOVA $F_{4,76} = 1.37$, $P = 0.25$), and similar in 1993 with the differences being entirely due to Ferreira (Fig. 1B, ANOVA $F_{4,93} = 4.37$, $P = 0.003$; post-hoc comparison, Scheffe test $P < 0.05$). Laying date was included to look for an effect of time of season on the parasitism rate.

Values in tables and text are means ±SE. Data were z-transformed before ANOVA and multiple regression procedures using square root and arcsine transformations (Sokal and Rohlf 1995).

RESULTS

SPATIAL AND TEMPORAL PROXIMITY AND PARASITISM PROBABILITY

Logistic regression showed that the number of temporal neighbors and density index had a significant effect on the probability of a nest of being parasitized in 1993. A logistic regression model incorporating these two variables described the data as well as a model with all the variables (Table 1; final model $\chi^2 = 24.84$, $P < 0.001$. However in 1992, only the number of temporal neighbors significantly affected parasitism probability (Table 1; $\chi^2 = 11.03$, $P < 0.001$). Laying date and cuckoo density had no significant effect.

Since these two variables affect parasitism probability, they could also be good predictors of the number of cuckoo eggs per nest. We assumed that nests with a high probability of being parasitized will receive a greater number of cuckoo eggs than nests with a small probability of being parasitized. A backward, stepwise multiple regression using the same variable set as used in the logistic regression as dependent and independent variables gave two different results for 1992 and 1993. In the first year only the number of temporal neighbors was included in the model ($R = 0.34$, df = 4, 111, $P < 0.001$), but in 1993 both number of temporal neighbors and density index were in the model ($R = 0.44$, df = 4, 130, $P < 0.001$; partial regression coefficient for number of temporal neighbors $r = -0.33$, $P < 0.001$; partial regression coefficient for density index $r = -0.30$, $P < 0.001$).

SPATIAL AND TEMPORAL PROXIMITY AND MAGPIE BREEDING SUCCESS

Brood parasitism has a significant impact on the breeding success of magpie pairs because most parasitized nests do not fledge any magpie chicks (Soler et al., in press). Magpie breeding success in the two years of this study was severely affected by the number of cuckoo eggs in the nest, decreasing with an increasing number of cuckoo eggs and very low in all parasitized nests (Fig. 2).

As the number of cuckoo eggs was related to the nest density index and number of temporal neighbors, we expected that these variables would correlate with magpie breeding success. There was no significant correlation in 1992 (multiple $R = 0.18$, $P > 0.05$), but in 1993 both number of temporal neighbors and density index were negatively correlated with breeding success ($R = 0.37$, df = 2, 77, $P = 0.003$; partial r for number of temporal neighbors $= -0.30$, $P = 0.007$, partial r for density index $= -0.24$, $P = 0.04$).

MAGPIE SOCIAL ORGANIZATION

Magpie nests showed significant differences in nearest neighbor distance between plots (Fig. 3; $F_{4,101} = 7.4$, $P < 0.001$ for 1992 and $F_{4,130} = 12.4$, $P < 0.001$ for 1993). However, a post-hoc comparison revealed no significant differences for La Calahorra, Fuente Alamo and Ferreira on one side, and Carretera and Hueneja on the other side (Scheffe test, $P > 0.05$, both years). Thus, we considered three high-density plots (more than 15 pairs/km^2; Fig. 3), and two low-density plots (less than 10 pairs/km^2 Fig. 3) that differed significantly in density (Fig. 4; $t = 2.63$, df = 130, $P = 0.009$ in 1992; $t = 6.24$, df = 155, $P < 0.001$ in 1993) and nearest neighbor distances (141.9 ± 11.7 m and 300.7 ± 41.1 m, $t = 5.04$, df = 104, $P < 0.001$ for 1992; 133.3 ± 8.4 m and 293.2 ± 29.9 m, $t = 7.09$, df = 133, $P < 0.001$ for 1993).

With respect to synchrony, mean number of temporal neighbors differed between plots in both years ($F_{4,118} = 17.5$, $P < 0.001$ for 1992 and $F_{4,135} = 25.8$, $P < 0.001$ for 1993; Fig. 4), the differences being due to La Calahorra in 1992 and La Calahorra and Hueneja in 1993 (post-hoc comparison, Scheffé test $P < 0.05$; Fig. 4).

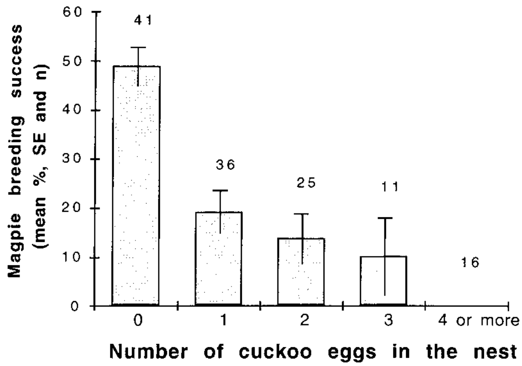

FIGURE 2. Magpie breeding success in relation to the number of cuckoo eggs layed in the nest. Horizontal lines are standard errors and numbers above the bars are sample sizes.

Statistical comparisons of parasitism rate or magpie breeding success between plots are not possible due to sample sizes. However, such data may serve as an indicator of the trends. As expected under the hypothesis tested, the plot with the highest mean number of temporal neighbors within the high-density plots suffered the lowest parasitism rate in both years (Figs. 3 and 4).

NEST DEFENSE

We only occasionally saw magpies chasing cuckoos (Fig. 5). Attacks happened more often in high density plots than in low density plots, but differences are not significant (8.2% against 5.7% in 1992; 9.3% against 3.7%, $\chi^2 = 0.19$ and $\chi^2 = 1.00$ respectively, $P > 0.05$). Nine of the nineteen observations of chases were recorded in La Calahorra. We have never seen more than two magpies chasing a cuckoo simultaneously, so group defense either does not exist or is rare in these populations.

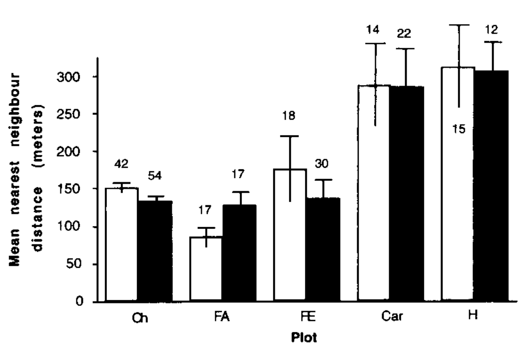

FIGURE 3. Mean nearest neighbor distances for each plot and year. For further explanations see Figure 1.

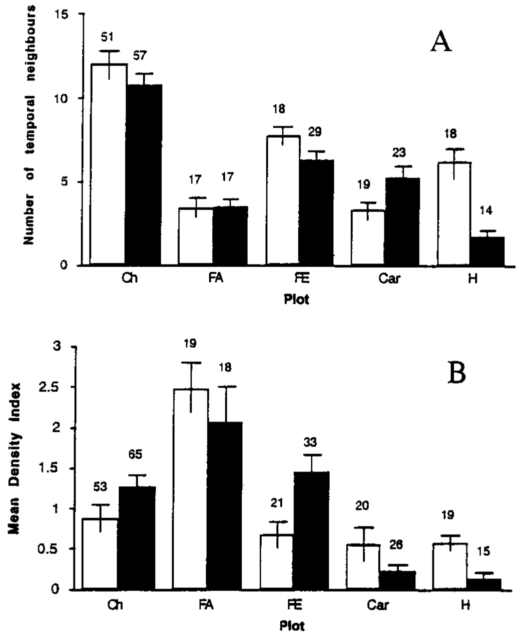

FIGURE 4. Mean number of temporal neighbors (A) and density index (B) for each plot and year. For further explanations see Figure 1.

DISCUSSION

PARASITISM RATE AND TEMPORAL AND SPATIAL PROXIMITY

We hypothesized that spatial and temporal proximity between magpie nests should lower the risk of parasitism. Our data support this: nests with synchronously breeding neighbors and nests at higher densities were either not parasitized or received a lower number of cuckoo eggs. The role of breeding synchrony was clear—it increased the chances of avoiding parasitism because most nests were available simultaneously.

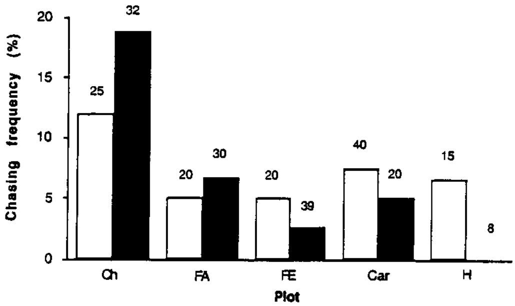

FIGURE 5. Chasing frequency (as percentage of total number of observations) of cuckoos by magpies for each plot and year. For further explanations see Figure 1.

Great Spotted Cuckoo females lay their eggs on alternate days in three series of three to six eggs, with some days between each series (Payne 1977, Arias de Reyna et al. 1982). They lay most of their eggs during the egg-laying period of the magpies and less frequently when the clutch is finished or before clutch initiation (Soler et al., in press). Thus, magpies laying synchronously dilute the effect of parasitism (the "swamping effect," Clark and Robertson 1979), because there are more active nests than a parasite can parasitize. In addition, as the number of magpie pairs laying simultaneously increases, the possibilities for the Great Spotted Cuckoo to find a host nest in the right stage decreases.

The effect of spatial proximity was only significant in one year. It is less clear how spatial proximity decreases the probability of parasitism. It has been proposed that high density aggregations of hosts may allow group defense or more effective nest defense (Clark and Robertson 1979, Freeman et al. 1990). In dense plots, hosts may easily become aware of the presence of the parasite and mob it more quickly and/or in groups. We do not have data to test this prediction, but nest defense against parasites seems to be infrequent and magpies showed no group defense. However, if nest defense is the mechanism underlying the relationship between density and probability of parasitism, the inconsistency of this relationship between years may be due to a different ecological conditions. Magpies in our study area leave their territory to feed, giving the cuckoos a chance to approach the nest undetected (pers. observ.) and the duration of these absences may vary between years as a function of food availability near the nest.

The absence of nest defense might be an effect of the short history of sympatry between magpies and Great Spotted Cuckoos. Guadix is presumably a recently colonized area (Soler 1990, Soler and Møller 1990, Soler et al. 1994, but see Zuniga and Redondo 1992), and it has been reported that behavioral responses to parasites, including nest defense (Briskie et al. 1992), vary between populations that have been exposed to parasitism for different lenghts of time (Soler and Møller 1990). Indeed, magpies attack Great Spotted Cuckoos frequently in areas of ancient sympatry (Alvarez and Arias de Reyna 1974).

Breeding synchrony and proximity to other nests are advantageous to magpies, by diminishing the probability of parasitism and enhancing the probability of successful breeding (Fig. 2). There was a positive correlation between both the number of temporal neighbors and the density index and breeding success in 1993. The absence of this correlation in 1992 may be due to the absence of a significant relationship between density index and parasitism in that year and to the fact that breeding success is related also to other variables such as territory quality, time in the season, or food availability.

MAGPIE SOCIAL ORGANIZATION AND PARASITISM RATE

The spatial dispersion pattern of magpies varied between plots in our study area. This variability is primarily due to ecological factors such as habitat type and food availability (Birkhead et al. 1986, Birkhead 1991). From the results obtained in this study, we expected that the rate of parasitism would be low in synchronous, dense plots, and high in asynchronous, low-density plots. Data suggest a trend in this direction, but the results do not fit the prediction exactly, as high-density plots (Fuente Alamo, Ferreira) had parasitism rates similar to these of low density plots. However, these high density plots were characterized by a low number of temporal neighbors due to their small size. Thus, the number of pairs laying at the same time in a plot will depend on both synchrony and the total number of pairs. Very small plots such as Fuente Alamo will have few temporal neighbors, thus weakening the "swamping effect."

Finally, differences in parasitism pressure may be another factor explaining the different spatial patterns of north and south European magpie populations. Spatial proximity and synchrony are advantageous for magpies breeding in sympatry with the Great Spotted Cuckoo and thus we expect to find magpies breeding close together and synchronously. However, density and synchrony are constrained by other ecological factors such as food availability and habitat structure. Thus, heterogeneity in nest distribution may partially account for differences in parasitism rates between plots in a region. In low-density plots magpie density may be limited by habitat quality and/or food availability and the low reproductive success due to parasitism may decrease magpie density over time. Magpies would be able to nest close together and synchronously only in plots rich in food and nest sites, but they then face other potential risks such as cuckoldry or increased competition for food.

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