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Cooperative breeding in carrion crows reduces the rate of brood parasitism by great spotted cuckoos

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Interactions between brood parasites and hosts can lead to coevolutionary arms races, whereby hosts evolve defences such as ejection of alien eggs and nest defence, and parasites respond with mimetic eggs and shorter laying times. However, little is known about interactions between brood parasites and cooperatively breeding hosts. The presence of several caregivers may either benefit the brood parasite by increasing reproductive success or be a disadvantage, if helpers improve nest defence. We addressed these hypotheses in cooperative carrion crows, *Corvus corone corone*, and their brood parasite, the great spotted cuckoo, *Clamator glandarius*, whose chicks are raised together. Parasitism rate by great spotted cuckoos was inversely correlated with crow group size and unassisted pairs were most likely be parasitized, in spite of being relatively rare. Moreover, in the nests of unassisted pairs, cuckoo chicks enjoyed a greater age advantage with respect to crow chicks compared to nests of larger groups, suggesting that parasitic females could not optimize laying date in nests with helpers. Although multiple caregivers increased cuckoo chick survival, this merely compensated for the smaller age advantage that parasitic chicks enjoyed in nests with helpers compared to those of unassisted pairs. Our results indicate that the presence of helpers reduces the cuckoo's laying performance, providing the first indication that cooperative breeding may protect against brood parasitism. This might occur in crows because the presence of helpers allowed incubating females to increase the time spent at the nest, reducing the parasite's opportunities to lay eggs.

Avian brood parasites lay their eggs in the nests of other bird species (the hosts), which pay a fitness cost from raising the parasitic chicks (Rothstein 1990). Parasitism costs for the host are often high because (1) female parasites may remove or damage the host eggs, (2) parasitic chicks may eject all other eggs and chicks from the nest, (3) parasitic chicks may outcompete host nestlings for food, when raised alongside them (Davies et al. 1998; Kilner 2003), and (4) provisioning parasitic nestlings often requires longer and more demanding care than raising the host's own brood (Rothstein 1990). These high fitness costs favour the evolution of host defences such as recognition and ejection of alien eggs and/or mobbing of parasitic females (Davies & Brooke 1989a; Soler et al. 1999b; Roskaft et al. 2002; Aviles et al. 2004; Moskat 2005). Host–parasite interactions can thus escalate into coevolutionary arms races of adaptation and counteradaptation, whereby the hosts evolve finer mechanisms of egg discrimination and nest defence, and the parasites respond with better egg mimicry and laying strategies (Davies & Brooke 1989a, b; J. J. Soler et al. 2001). Parasitic strategies to improve reproductive success include choice of suitable host species (Soler et al. 1999a) and choice of host nests, where nests at the most advantageous laying stages and/or built by high-quality pairs are preferentially parasitized (Soler et al. 1995).

While parasite/host coevolution has been studied in detail in biparental host species, little is known about the interactions between brood parasites and cooperatively breeding hosts. In cooperative bird species, a variable number of helpers assists the breeding pair in provisioning the young and defending the nest against predators (Cockburn 1998). In many cases, the presence of helpers increases the annual reproductive success of the group by augmenting the number of fledglings produced (Magrath 2001; Richardson et al. 2002; Covas & du Plessis 2005; Woxvold & Magrath 2005; Canestrari et al. 2008) or by enhancing their body condition (Hatchwell et al. 2004; Valencia et al. 2006). Cooperative hosts might be preferred by brood parasites because the increased provisioning frequency of larger groups makes the nest more conspicuous, and/or because it may improve the reproductive success of the parasite (Rowley & Russell 1990; Poiani & Elgar 1994). Cooperation might therefore be disadvantageous for the

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host in terms of the risk of being parasitized. On the other hand, cooperative groups might possess better defences against parasites, if helpers contribute to ejecting alien eggs, guarding the nest and evicting intruders, or increase the nest attendance of the breeding female, by provisioning her during incubation, and hence reducing the cuckoos' laying opportunities.

The effect of cooperative breeding on brood parasitism rate has been specifically addressed by Poiani & Elgar (1994), who compared parasitism rates of five cuckoo species on cooperative and noncooperative hosts in Australia, but their analyses did not reveal a clear pattern. The authors suggested that the different durations of the host–parasite interactions may have masked a general trend, and that within-species comparisons in parasitized populations where both unassisted pairs and cooperative groups are available simultaneously may shed light on the relationship between host social system and brood parasitism. However, studies on the effect of host group size on brood parasitism are scarce. The superb fairy-wren, *Malurus cyaneus*, and the splendid fairy-wren, *Malurus splendens*, are cooperatively breeding Australian birds (Rowley et al. 1991; Dunn et al. 1995) and are, respectively, the primary and secondary host of Horsfield's bronze-cuckoo, *Chalcites basalis* (Langmore & Kilner 2006). In both host species, the risk of parasitism does not change with group size (Brooker & Brooker 1996; Langmore & Kilner 2006), suggesting that host group size does not influence brood parasitism.

We have studied a cooperative population of carrion crows, *Corvus corone corone*, in northern Spain and its brood parasite, the great spotted cuckoo, *Clamator glandarius*. Carrion crows in northern Spain have helpers at the nest in about 75% of territories, where they form groups of up to nine individuals containing both retained offspring and related immigrants from other territories (Baglione et al. 2002). Helpers participate in chick provisioning and territory defence (Baglione et al. 2002; Canestrari et al. 2005), and group size is positively and linearly correlated with the reproductive success of the group, owing to the greater provisioning effort by several caregivers (Canestrari et al. 2008). The carrion crow is an important secondary host of the great spotted cuckoo, an avian brood parasite specialized on corvids (Soler 1990); its primary host in Spain is the magpie, *Pica pica* (Soler 1990; Soler et al. 1998). This parasite lays synchronously with its hosts but, owing to the shorter incubation period of cuckoo eggs, parasitic chicks hatch earlier and gain an age advantage over the host nestlings (Soler et al. 1998). Great spotted cuckoo chicks do not evict other eggs and chicks from the nest, and may be raised alongside host nestlings. However, parasitic chicks often outcompete magpie chicks for food and make them starve to death within a few days of hatching, while crow nestlings generally survive until fledging (M. Soler et al. 2001). When parasitizing magpies, great spotted cuckoos do not choose host nests at random, but preferentially lay eggs in nests built by high-quality pairs. Parasitic females probably base their choice on magpie nest size, which is positively correlated with other measures of pair quality (Soler et al. 1995).

In this study, we used data from 99 crow reproductive territories that were each monitored over 12 years to investigate the relationship between host group size and brood parasitism. If cooperative behaviour enhanced cuckoo reproductive success, cuckoo females would be expected to prefer pairs with helpers. However, cooperative groups might possess more efficient defences in response to brood parasitism compared to unassisted pairs, in which case we expect parasitism rate to decrease as host group size increases, irrespective of the effect of group size on parasite reproductive success. To test whether the cooperative behaviour of the crow hosts represents a benefit or a disadvantage for the great spotted cuckoo, and to evaluate the costs of parasitism to the host, we analysed (1) the relationship between host group size and parasitism rate, (2) the effect of group size on the cuckoo's opportunities to lay eggs, measured as the time spent outside the nest by incubating females, (3) the effect of crow group size on cuckoo reproductive success, and (4) the effect of parasitism on annual crow reproductive success.

METHODS

Study Area and Population

We studied a cooperative population of carrion crows in a 45 km^2 rural area in northern Spain (42° N, 5° W) with a traditional low-intensity agricultural landscape characterized by a mosaic of crops, meadows, poplar and pine plantations, scrub, oak forest patches and uncultivated land. Since 1995, we have banded 633 nestlings (captured in the nest just prior to fledging, i.e. when the oldest chick was 28–30 days old) and 105 adult crows with colour rings and/or wing tags, which did not affect survival (Caffrey 2000; Canestrari et al. 2007). During the study period (1995–2006), on average 73.2% (range 58.5–80.9%) of territories every year were occupied by social groups of three to nine individuals, while the remaining territories were held by pairs (Baglione et al. 2002). Helpers (up to three per nest, as some group members refrain from provisioning the chicks) participate in building the nest, feeding the incubating female and the chicks, and defending the territory against intruders and predators (Baglione et al. 2002; Canestrari et al. 2005). Crows live year-round in all-purpose nonoverlapping territories (average size $\pm$ SE $= 0.13 \pm 0.01$ km^2), which are defended from conspecific intruders (Baglione et al. 2005). Territory boundaries are constant over years with crows consistently using a few traditional nesting sites, as trees suitable for nesting are scarce. Individual territories are therefore recognizable across years even when crows are unbanded, or when banded groups are replaced by unbanded individuals. From late March to mid-May, breeding females may lay one to seven eggs ($\overline{X} \pm \mathrm{SE} = 4.6 \pm 0.05$) per breeding attempt, but about 70% of attempts fail (Canestrari et al. 2008). When this happens at the egg or hatching stage, crows may renest for a total of three nesting attempts per season, but only one successful brood ($\overline{X} \pm \mathrm{SE} = 2.4 \pm 0.06$ fledglings) can be raised every year (Canestrari et al. 2008). Group size positively affects the reproductive success of a group, increasing the probability of renesting after an early nest failure, the probability of raising at least one chick per season and the number of fledglings per successful attempt (Canestrari et al. 2008).

The great spotted cuckoo is a brood parasite specialized on corvids. This parasite strongly reduces magpie reproductive success through egg destruction during laying and starvation of host chicks, especially when the parasitic chicks hatch earlier than the host's chicks, but costs of parasitism for carrion crows may be much lower (Soler 1990; Soler et al. 1996).

Nest and Brood Parasitism Survey

At the beginning of each breeding season (end of March) we surveyed all territories in the study area to find new nests. Afterwards, regular visits (about once a week) allowed detection of late nesting attempts. Until egg laying was complete, all nests were inspected every 1–2 days to record the date of egg laying, the clutch size and the presence and number of parasitic eggs. Cuckoo eggs were easily distinguishable from crow eggs by their smaller size and different colour: of 2206 eggs of both species that hatched, none was mistakenly assigned. After 20 days of incubation, nests were visited daily until the last egg was hatched to record hatching sequence and hatching success. Afterwards, nests were visited regularly to monitor the survival of cuckoo and crow chicks. If a nest

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failed at the egg or hatching stage, the territory was searched for new nests. All nests were visited with the same frequency. Regardless of group size, adult group members invariably reacted to nest inspection by fleeing and perching at a safe distance, until we left the territory. To minimize possible adverse effects of our inspections on incubation or brooding, we avoided visiting the territories during bad weather. All bird manipulations were authorized by Junta de Castilla y León.

Territories and Groups Survey

During each breeding season (March–July), we monitored group size and composition (presence or absence of banded birds and their identity) on the surveyed territories. In 64–79% of territories every year this was done in March, just before egg laying, by observing the groups from a favourable spot for at least 1 h. In all territories, group members were also counted during visits for routine data collection (egg-laying sequence, nestling growth, fledging success). Since group members usually form a cohesive group, these short visits to the territories (15–30 min, repeated 5–10 times throughout the breeding season) provided reliable information on group size. When a territory remained vacant during a whole breeding season, or when group size was unknown, we excluded the data point from that particular year in the analyses. Information on group size and presence or absence of parasitic eggs was collected for 1114 nests in 829 territory-years (99 different territories; mean number of sampled breeding seasons per territory $\pm$ SE $= 7.32 \pm 0.36$), of which 114 nests were parasitized. Fluctuations in group size ($\pm$one individual) within a breeding season, caused by the death of a group member or, more often, movements to and from the territory by juveniles prospecting neighbouring areas, were recorded in 33 group-years. In these cases, we entered in the analysis the minimum group size recorded, because prospecting individuals typically do not contribute much to allofeeding and territory defence (Baglione et al. 2006). Removal of these groups from the analyses did not qualitatively change the results.

Between 1995 and 2000, we measured the proportion of time spent inside and outside the nest by the incubating female in 22 groups of known size. To do so, we carried out on average $\pm$ SE 78 ± 5.8 min of observations per group with binoculars and 20×60 spotting scopes from favourable observation spots 400 m away from the nest. For 13 of these nests, we mapped the movements of the incubating female when she left the nest (1–5 data points per female; 33 in total) and calculated her distance to the unattended nest. For 16 nests, we could also count feeding visits to the incubating female by other group members.

Statistical Analyses

Unless stated otherwise, we analysed all data with mixed models (GenStat 10.0, VSN International Ltd, Hemel Hempstead, U.K.), which allow the inclusion of both fixed and random terms. Data collected in the same territory across years are not independent because intrinsic characteristics of the territory (e.g. resource abundance, predator density) may affect brood parasitism rates. By fitting 'territory identity' as a random term into all analyses, we controlled for the effect of territory quality, assuming that territories retain the same relative quality between seasons. Potential explanatory variables that gave nonsignificant results ($P > 0.1$) were sequentially eliminated until the model only included those terms for which elimination would have significantly reduced the explanatory power. Significant probability values were derived from having all significant terms fitted in the model together, whereas those of nonsignificant terms were obtained by individually reintroducing each nonsignificant term to the minimal model (Crawley 2002; Russell et al. 2003). Only interactions that were biologically meaningful were entered in the models (see description of specific analyses). In the Results, values for nonsignificant interactions are omitted. For each question addressed, we analysed a data set that contained only the relevant information (see Table 1).

To analyse the factors affecting the crows' probability of being parasitized, we fitted a generalized linear mixed model (GLMM) with binomial distribution and logit link function with a dichotomous dependent variable (parasitized/not parasitized), and the following explanatory variables: group size, number of reproductive attempt (first, second, third attempt within year), annual parasitism rate (calculated as the number of parasitized nests/number of all nests for that particular year) and the interaction between group size and annual parasitism rate. This analysis was first carried out on the complete sample of all territories studied, and was then repeated using the subsample of territories that were parasitized at least once during the 12-year period, to exclude territories that may have been unsuitable for great spotted cuckoos. Subsequently, we analysed with a restricted maximum likelihood model (REML) the factors influencing the number of cuckoo eggs laid per parasitized nest, fitting the same variables as in the previous analyses. Territory identity was entered as a random factor in these analyses, but year was not included because the variable measuring the annual parasitism rate already accounted for the relevant variation among years. The relationship between nest attendance by the incubating female (i.e. the proportion of time spent at the nest) and group size, and between the rate of feeding visits to the incubating female and group size, were analysed with Spearman rank correlations.

To investigate the influence of crow group size on cuckoo reproductive success we took the following steps. First, we ran an REML to analyse the factors affecting the number of cuckoo eggs hatched, entering the following explanatory variables: group size, number of reproductive attempt, number of cuckoo eggs, total number of eggs in the nest as a measure of competition for incubation, interaction between group size and number of eggs, and interaction between number of cuckoo eggs and number of crow eggs; random factors: year and territory. Second, we ran a GLMM

Table 1
Description of sample sizes used in the statistical analyses

Question	Dependent variable	No. of territories	No. of data points
Effect of group size on cuckoo reproductive success	(1) Number of cuckoo eggs hatched	50	116 attempts
	(2) Individual cuckoo fledging success (hatched chicks only)	50	73 cuckoo chicks
	(3) Age difference between hatched cuckoo and crow chicks	36	79 cuckoo chicks
	(4) Number of cuckoo chicks fledged	36	116 attempts
Effect of parasitism on crow reproductive success	Total number of crow chicks produced (only territories that were parasitized at least once during the study period)	51	717 attempts
Effect of group size on parasitism rate	(1) Presence/absence of parasitic eggs (all territories in the study area)	99	1114 attempts
	(2) Presence/absence of parasitic eggs (only territories that were parasitized at least once during the study period)	51	739 attempts
	(3) Number of cuckoo eggs per parasitized nest	51	116 attempts

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with binomial distribution and logit link function to investigate the factors affecting the individual cuckoo fledging success in nests where at least one cuckoo egg hatched. The dichotomous dependent variable, calculated for each individual chick hatched, was fledged/dead; the explanatory variables were: group size, number of reproductive attempt, number of cuckoos hatched, total number of chicks hatched, age difference between cuckoo and first-hatched crow chick, and interaction between age difference and group size; random factors: year and territory. Age difference between great spotted cuckoo and crow chicks is an important predictor of cuckoo fledging success, as parasitic chicks that hatch earlier than crow chicks have higher survival probabilities (Ariasdereyna 1998; M. Soler et al. 2001). Therefore, in the third analysis, we ran an REML to test the factors affecting the age difference between each cuckoo chick and the first crow hatched, which indicates to what extent the cuckoo female could lay her eggs at the optimum time (explanatory variables: group size, number of reproductive attempt and hatching order of cuckoo eggs; random factors: year and territory). Fourth, we analysed how the effects of group size on the previous steps of cuckoo reproduction considered (hatching success, individual fledging success and age difference with host nestlings) combined to influence the total number of cuckoo fledglings produced. To do so, we analysed in an REML the factors affecting the total number of cuckoos fledged in parasitized nests, entering the following explanatory variables: group size, number of cuckoo eggs laid, number of reproductive attempt, and total number of eggs in the nest as a measure of competition; random factors: year and territory. Finally, we ran an REML to test the effect of parasitism on crow reproductive success, entering the following explanatory variables: group size, number of crow eggs laid, number of reproductive attempt, presence or absence of parasitic eggs, interaction between group size and presence or absence of parasitic eggs; random factors: year and territory.

Ideally, our mixed models should have also included 'group identity' and/or 'breeders' identity' to account for individual variability in reproductive quality. Unfortunately, determining a biologically relevant criterion to define 'group identity' is difficult, because changes in group composition across years are gradual and occur by many different routes. Identifying breeders is also troublesome in this complex society, where polygamous mating is frequent (Baglione et al. 2002). Restricting our sample only to groups where changes in composition or turnover of breeders could be documented would have dramatically reduced the power of the analyses. In addition, we believe that the variable 'territory identity' partially accounts for core membership of the group, because crows are long lived and turnover of entire groups occurs in only 14% of territories every year in this population (Baglione et al. 2005).

RESULTS

Over the 12-year study period, the percentage of nests that were parasitized varied between 2.2% and 31.4%. Before 2003, parasitism rate remained relatively low (with a maximum of 7.4% of nests parasitized), while in the last 3 years of the study, it increased steadily from 11.9% to 31.4%. Cuckoos laid one to three eggs per nest (average = 1.53), but we do not know whether one or several females laid eggs in the same nest.

Host Group Size, Parasitism Rate and Incubating Female's Nest Attendance

After controlling for the significant effect of territory identity on the probability of being parasitized, we found a negative effect of group size (Table 2), with pairs being the most parasitized group size (Fig. 1). The probability of being parasitized increased with annual parasitism rate for all group sizes, but was not influenced by the reproductive attempt or by the interaction between group size and annual parasitism rate. These results held also when we restricted the sample to those territories that were parasitized at least once over the study period. In parasitized nests, the number of cuckoo eggs was independent of group size, annual parasitism rate, reproductive attempt and the interaction between group size and annual parasitism rate (Table 2). This means that as the annual parasitism rate increased, more nests were parasitized, but the number of eggs laid per nest did not change, and that nests of parasitized pairs did not contain more cuckoo eggs than those of parasitized groups.

A cuckoo female's opportunities to lay eggs, measured as the proportion of time that the incubating female spent outside the nest, decreased as host group size increased (Spearman correlation: $r_S = -0.65$, $N = 22$, $P = 0.001$; Fig. 2). When leaving the nest,

Table 2
Factors affecting the probability of parasitism

Model terms	*F*	*df*	*P*	Random term estimated variance component±SE	Average effect±SE
Probability of being parasitized (all territories)					
Full model					
Territory identity*				0.61±0.22	
Group size	5.05	1, 1024.1	0.025		
Annual parasitism rate	100.79	1, 1136.6	<0.001		
Nesting attempt	0.96	1, 1129.5	0.33		
Minimal model					
Constant					−2.09±0.13
Group size					−0.21±0.09
Annual parasitism rate					7.99±0.79
Number of cuckoo eggs in parasitized nests					
Full model					
Territory identity*				0.005±0.04	
Group size	1.62	1, 94.9	0.21		
Annual parasitism rate	0.04	1, 105.1	0.84		
Nesting attempt	1.11	1, 105.8	0.29		

P values for all variables entered in the analyses are given in 'full model'. Variables with a nonsignificant *P* value were sequentially removed until only significant terms were included ('minimal model'). Average term effects ± SE are given only for significant explanatory variables included in the minimal model.
* Random terms.

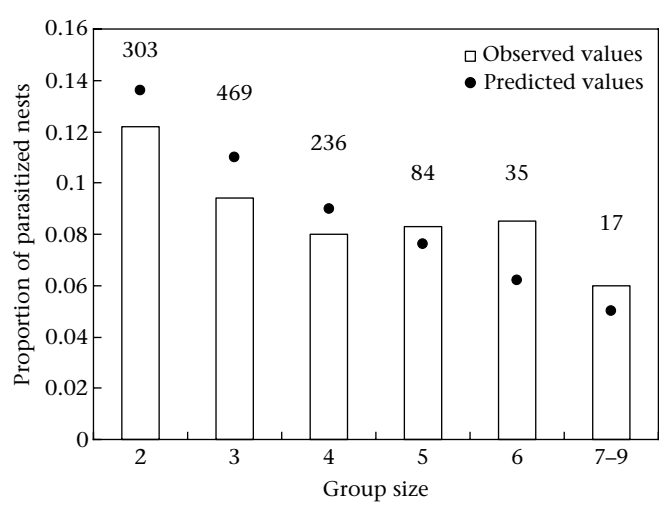

Figure 1. Proportion of crow nests that were parasitized in relation to group size. Observed values and predictions from the model are shown. Sample sizes are given above the bars.

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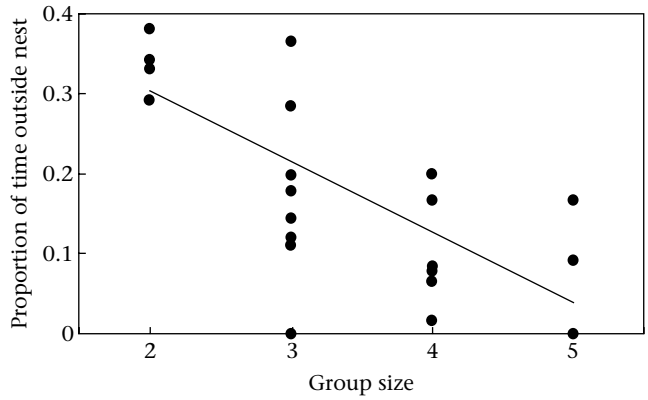

Figure 2. Correlation between group size and proportion of time spent outside the nest by the incubating female.

incubating females typically joined the foraging group on the ground, at an average distance ± SE from the nest of 174.2 ± 14.8 m (range 48–304 m, $N = 13$, each datum representing the average for every female). The nest was left unattended until the breeding female resumed incubation. Group size did not significantly affect the average distance between the foraging female and her unattended nest (Spearman correlation: $r_S = 0.23$, $N = 13$, $P = 0.45$). During incubation, provisioning of the incubating female by other group members increased with group size (Spearman correlation: $r_S = 0.51$, $N = 16$, $P = 0.04$).

Great Spotted Cuckoo Reproductive Success and Host Group Size

The results described here are summarized in Table 3. On average, 0.93 cuckoo eggs hatched per parasitized nest (range 0–3) and 0.56 cuckoo chicks (range 0–2) fledged. Only 36% of all cuckoo eggs ($N = 179$) laid in crow nests produced a fledgling. Of the 70 unhatched cuckoo eggs (39% of all cuckoo eggs laid), 53 disappeared together with all host eggs, suggesting that the whole clutch was depredated. Of the remaining 17 parasitic eggs, six were infertile, and 11 (6.14% of all cuckoo eggs laid) disappeared before hatching. The number of cuckoo eggs hatched was strongly correlated with the number of cuckoo eggs laid, while it was not affected by the total number of eggs in the nest or by group size. All interactions were nonsignificant. Parasitic eggs hatched between 8 days earlier and 7 days later than the first-hatched host nestmate. In nests that reached hatching stage, parasitic chicks with a greater age advantage over host nestmates had a higher fledging probability. After we controlled for the significant effect of age difference with crow chicks, individual cuckoo fledging success was positively correlated with group size (Fig. 3a). In other words, when we compared cuckoo chicks with the same age difference with host chicks, those raised by cooperative groups had higher fledging success. However, cuckoo chicks in nests of pairs hatched with a significantly greater age advantage over host chicks than those in nests with helpers (Fig. 3b). The sum of these contrasting effects on two important factors affecting cuckoo survival meant that the total number of cuckoos raised per nest did not vary with crow group size (Fig. 3c), probably because the higher provisioning frequency by larger groups compensated for the smaller age advantage of parasitic chicks in their nests.

Effect of Parasitism on Crow Reproductive Success

The presence of parasitic eggs did not significantly affect the number of crow fledglings produced ($F_{1,333.1} = 0.22$, $P = 0.64$). The number of crow fledglings produced was positively correlated only with the number of crow eggs laid ($F_{1,514.6} = 21.63$, $P < 0.001$) and with group size ($F_{1,514.6} = 8.14$, $P < 0.001$). Similar results were obtained when we tested the effect of the number of cuckoo eggs laid, or the number of cuckoo eggs hatched.

Table 3
Factors affecting great spotted cuckoo fledging success

Model terms	*F*	*df*	*P*	Random term estimated variance component±SE	Average effect±SE
Number of eggs hatched (REML)					
Full model					
Territory identity*				−0.05±0.04	
Year*				0.02±0.03	
No. of cuckoo eggs laid	94.89	1,103.2	<0.001		
Group size	0.11	1,87.5	0.74		
Nesting attempt	0.1	1,101.2	0.79		
Clutch size	0.29	1,53	0.59		
Minimal model					
Constant					0.93±0.07
No. of cuckoo eggs					0.94±0.09
Individual cuckoo fledging success, only hatched chicks (GLMM with binomial distribution)					
Full model					
Territory identity*				3.43±1.75	
Year*				1.81±1.6	
No. of cuckoo eggs hatched	0.09	1,62.2	0.77		
Total No. of chicks in nest	1.88	1,63.9	0.18		
Group size	6.10	1,64.1	0.02		
Nesting attempt	0.14	1,70.3	0.71		
Age difference between cuckoo and crow chicks	11.68	1,72.1	0.001		
Minimal model					
Constant					0.61±0.64
Group size					0.89±0.36
Age difference between cuckoo and crow chicks					0.52±0.15
Age difference between cuckoo hatchlings and first-hatched crow (REML)					
Full model					
Territory identity*				2.9±0.95	
Year*				1.32±1.02	
Group size	5.82	1,75.7	0.02		
Hatching order	139.83	1,75.7	<0.001		
Nesting attempt	0.19	1,42.9	0.67		
Minimal model					
Constant					2.08±0.49
Group size					−0.47±0.19
Hatching order					−1.74±0.14
Total number of cuckoo chicks fledged					
Full model					
Territory identity*				−0.01±0.06	
Year*				−0.007±0.02	
No. of cuckoo eggs laid	21.37	1,112.1	<0.001		
Group size	0.04	1,89.7	0.85		
Nesting attempt	0.96	1,107.6	0.33		
Clutch size	3.36	1,78.4	0.071		
Minimal model					
Constant					0.57±0.06
No. of cuckoo eggs					0.54±0.12

P values for all variables entered in the analyses are given in 'full model'. Variables with a nonsignificant *P* value were sequentially removed until only significant terms were included ('minimal model'). Average term effects ± SE are given only for significant explanatory variables included in the minimal model.
* Random terms.

DISCUSSION

Our study has shown that the rate of parasitism by great spotted cuckoos decreased with crow group size. This pattern could be

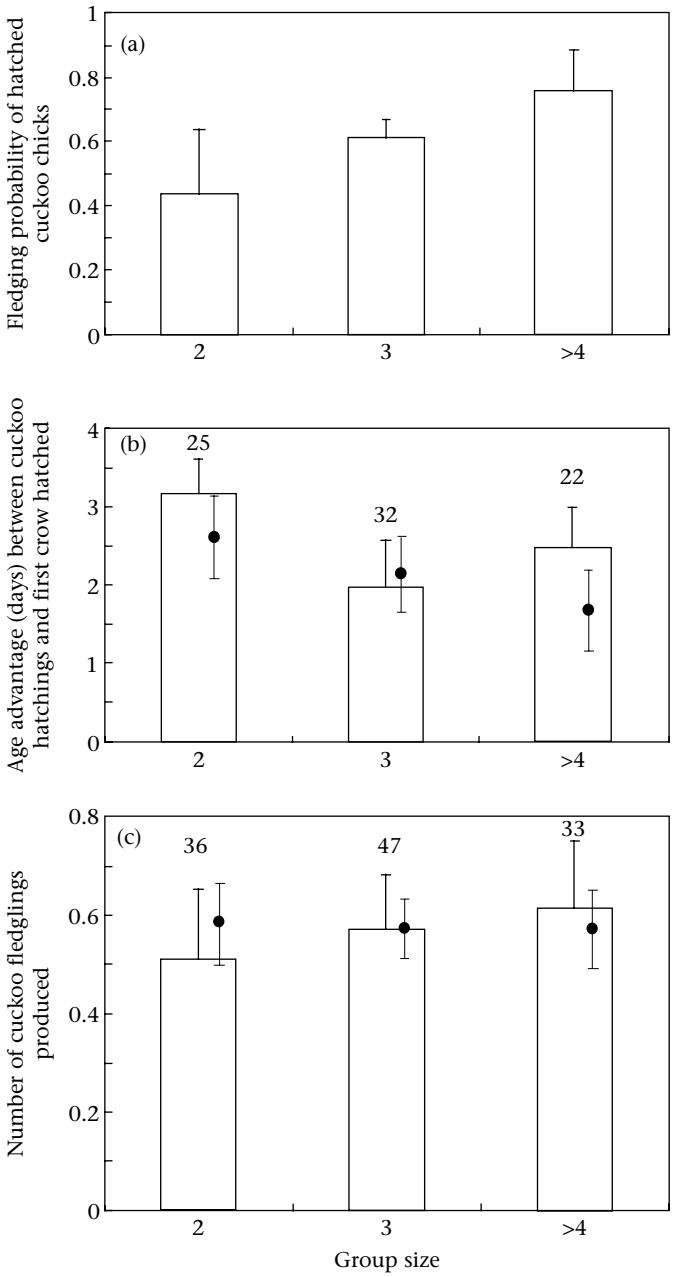

Figure 3. Effect of crow group size on (a) the fledging probability of cuckoo chicks that hatched successfully, after we controlled for the age difference between cuckoo and crow chicks (prediction of REML). (b) the age advantage between cuckoo hatchlings and the first-hatched crow in the nest, and (c) the total number of cuckoo fledglings produced (combination of the contrasting effects on the previous two stages). □: Observed values; ●: Predicted values. Sample sizes are given above the bars for (b) and (c).

caused by either choice of a preferred group size by the parasite, or better defence against parasitic adults by larger groups. Our results support the latter hypothesis. We found that cuckoo chicks hatched in nests of larger groups had higher fledging success than those raised by pairs, when we controlled for the difference in age between hosts and cuckoo chicks. In other words, when the age advantage with host chicks was equal, cuckoos survived better in groups with helpers at the nest. This result is consistent with the previous finding that the annual reproductive success of crows is positively correlated with group size (Canestrari et al. 2008), and indicates that the optimal strategy for great spotted cuckoos would be to lay their eggs at an optimal time in nests of cooperative groups. However, cuckoo chicks in nests of groups had a significantly smaller age advantage over host chicks than those raised by unassisted pairs, and were presumably less able to outcompete crow nestlings for food. These two effects counteracted one another, so that the number of cuckoos fledged per nest did not vary with crow group size.

Under these circumstances we might expect parasitic adults to lay their eggs randomly with respect to host group size, as alternative strategies currently do not confer different reproductive outcomes. Our results did not match this prediction. Nests of pairs were significantly more parasitized despite representing only 25% of available reproductive units (Baglione et al. 2002). The higher parasitism rate and the greater age advantage of cuckoo chicks in nests of unassisted pairs indicate that the presence of helpers made it difficult for the parasites both to pursue their optimal strategy and even to parasitize nests at random with respect to host group size. These results show for the first time that breeding in cooperative groups can reduce brood parasitism, potentially setting the stage for coevolutionary interactions between the host's social behaviour and the parasite's strategies to optimize timing of laying in nests of cooperative groups.

Active or Passive Defence?

In the case of the carrion crow, the presence of helpers is unlikely to constitute an active defence against great spotted cuckoos. Previous studies on different populations of this species showed that crows did not eject alien eggs from their nests and did not mob brood parasites (Yom-Tov 1976; Soler 1990). This may be because, for crows, the costs of hosting cuckoos in terms of annual reproductive success were small, and did not represent a strong selection pressure towards the evolution of active defences (M. Soler et al. 2001; this study). Alternatively, the interaction between great spotted cuckoos and crows might not have been for long enough to allow evolution of defences, as suggested by the theory of evolutionary lag (Davies & Brooke 1989b). Our observations suggest that such defensive strategies are likely to be negligible in our population, too. First, we have never observed adult crows mobbing great spotted cuckoos, even in the proximity of the nest. Second, our results on hatching success suggest that egg ejection by crows is at best rare, possibly involving only 6.14% of parasitic eggs that disappeared before hatching. However, the ejection rate might have been underestimated, as several cuckoo eggs might have been ejected a few hours after having been laid. Therefore, a higher ejection rate by larger groups might still explain the relatively higher number of parasitized pairs, but if this was the case we might expect to observe fewer cuckoo eggs in parasitized nests in larger groups than in parasitized unassisted pairs, which did not occur.

We suggest that the presence of helpers passively reduces brood parasitism rates. Similarly to the behaviour of cooperatively breeding green woodhoopoes, *Phoeniculus purpureus* (Radford 2004), crow helpers fed the incubating female, allowing her to spend more time at the nest rather than foraging on the ground with the rest of the group. Consistent with this idea, females' nest attendance increased with group size, reducing great spotted cuckoos' opportunities to lay their eggs. Another, nonexclusive, possibility is that cuckoo females have a preference for unassisted pairs because they are easier to parasitize. The alternative explanation that unassisted pairs may be preferred because of superior quality can be discarded, because they represent the least productive breeding unit, showing higher rates of nest failure and fewer fledglings produced per successful nest (Canestrari et al. 2008). Indeed, unassisted pairs are those that have been unsuccessful parents in the previous breeding seasons, producing no offspring that could delay dispersal and become helpers.

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Antiparasite Behaviour and the Benefits of Cooperation at the Nest

The general importance of parasites, including brood parasites, as selection pressures for shaping animal behaviour has long being recognized (Krause & Godin 1994; Poulin 2000). Because group living in birds may facilitate parasitic infection and cooperative breeding potentially exposes hosts to high rates of brood parasitism (see Introduction), helpers are expected to be involved in fighting parasites and such a role may contribute to maintaining a cooperative system over evolutionary time (Poiani & Elgar 1994). However, to our knowledge no studies have addressed this hypothesis, with the exception of Pacheco et al. (2006) who found that bell miner, *Manorina melanophrys*, helpers indeed show antiparasitic defence, removing dipteran larvae from the nest. Our results suggest that cooperative breeding represents a protection against brood parasites, even in the absence of specific defensive adaptations against them, and it is likely to represent a benefit of cooperation in species where brood parasitism conveys substantial costs. However, in other parasite–cooperative host systems, namely that of Horsefield's bronze-cuckoos parasitizing splendid fairy-wrens and superb fairy-wrens, group size was not correlated with parasitism rate (Brooker & Brooker 1996; Langmore & Kilner 2006). A critical difference between great spotted cuckoos and Horsefield's bronze-cuckoos is that the former's nestlings are raised alongside the host chicks and compete with them for food, while the latter's eject host eggs and chicks soon after hatching (Brooker & Brooker 1989). Relative timing of laying may therefore be more important for great spotted cuckoos, and any increase in host activity at the nest may represent for them a greater constraint than for Horsefield's bronze-cuckoos. Alternatively, larger group size may not lead to increased nest attendance in hosts of the Horsefield's bronze-cuckoos, as the host female is not fed as she incubates. More studies are needed to determine to what extent and under which circumstances host social organization influences brood parasitism, and to explore the generality of our results to other cooperative breeders.

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