

# Nest defense by Iberian azure-winged magpies (*Cyanopica cyanus*): do they recognize the threat of brood parasitism?

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The ultimate goal of nesting is the production of young and therefore predation and brood parasitism may constrain reproductive success. Breeding azure-winged magpies (*Cyanopica cyanus*) were exposed to mounts of an sparrowhawk (*Accipiter nisus*) (i.e. an avian predator on adult and fledged chicks), a female great spotted cuckoo (*Clamator glandarius*) (i.e. a brood parasite that also preys on eggs and chicks), and a mistle thrush (*Turdus viscivorus*) (i.e. an innocuous control) at different stages throughout the breeding cycle. In addition, the nest defensive behaviour of the azure-winged magpie and the common magpie (*Pica pica*) (the current favorite host for the great spotted cuckoo in Iberia) were compared. Azure-winged magpies behaved more aggressively (i.e. higher intensity and shorter latency to an aggressive response) towards the brood parasite and the predator mounts than towards the control. The number of individuals defending a nest was higher when exposed to a predator than to a control or a brood parasite. Aggressiveness against the brood parasite mount was not higher at laying as compared to other breeding periods. Azure-winged magpies defended more intensely than magpies when facing a great-spotted cuckoo, although the number of birds attacking the decoy was similar for both species. Thus, azure-winged magpies appear to perceive a different level of threat and defend their nests accordingly. We discuss the relevance of these results in explaining the current absence of brood parasitism in Iberian azure-winged magpies.

KEY WORDS: avian brood parasitism, *Cyanopica cyanus*, *Clamator glandarius*, nest defence, nest predation.

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## INTRODUCTION

Nest defense is a conspicuous component of parental care in birds that reduces loss caused by egg and nestling predation (ANDERSSON et al. 1980, GREIG-SMITH 1980, KNIGHT & TEMPLE 1986). Despite the obvious fitness benefits of nest defense, this behavior could be costly for parents due to the loss of time and energy (BIERMANN & ROBERTSON 1983). Indeed, while defending their nests, parents are unable to feed their offspring (e.g. CURIO 1975), and they may be injured or killed (e.g. CURIO & REGELMANN 1985), or attract other potential threats (e.g. ROBERTSON & NORMAN 1976, 1977; SMITH et al. 1984; see however GILL et al. 1997). The balance between these costs and benefits would determine the optimal level of defense for a given individual in a given situation (e.g. REDONDO 1989).

Nests of many passerine birds are simultaneously threatened by predators and brood parasites. Brood parasitism can impose the same or higher costs than predation (ROTHSTEIN 1990). For instance, parasitic cuckoo (*Cuculus canorus*) females often remove one or more host eggs from parasitized nests while laying, and the cuckoo hatchling ejects all host eggs or chicks from the nest (DAVIES 2000). Great spotted cuckoos (*Clamator glandarius*), however, can prey upon host eggs and chicks as a measure of extortion to force acceptance of parasitism (mafia behaviour, SOLER M. et al. 1995). Also, the shorter incubation periods and faster relative growth of great spotted cuckoo chicks as compared to their hosts result in a drastic reduction of host breeding success (SOLER J.J. & SOLER M. 2000). Hence, the level of nest defense exhibited by hosts of avian brood parasites may be affected by either brood parasitism and/or predation (SEALY et al. 1998, GRIM 2005). Indeed, GILL & SEALY (1996) reported that yellow warblers (*Dendroica petechia*) showed a more aggressive behaviour towards a mounted brown-headed cowbird (*Molothrus ater*) during their egg laying stage when cowbird parasitism occurs, but that the level of aggressiveness against the mounted parasite decreased after this period (see also NEUDORF & SEALY 1992). In addition, RØSKAFT et al. (2002) found that the level of nest defense and the rate of rejection of artificial cuckoo eggs (i.e. a defensive behaviour influenced by the strength of brood parasitism) were positively correlated among hosts of the European cuckoo, suggesting that nest defense may be shaped by brood parasitism.

The azure-winged magpie *Cyanopica cyanus* is a social small corvid with a disjunct distribution. It occurs widely in the eastern Palearctic and it is found in a smaller geographical area in Spain and Portugal (CRAMP & PERRINS 1994). Azure-winged magpies are sympatric over most of their range with common cuckoos and great spotted cuckoos in the Iberian Peninsula (CRAMP & PERRINS 1994). However, although the azure-winged magpie is frequently parasitized by the common cuckoo in the eastern Palearctic (NAKAMURA et al. 1998), no evidence of common cuckoo parasitism has so far been reported for the Iberian populations (reviewed in AVILÉS 2004, VALENCIA et al. 2005). There is, however, strong evidence of great spotted

cuckoo parasitism on Iberian azure-winged magpies in the recent past (FRIEDMANN 1964, SOLER J.J. et al. 2003), although this parasitic species preferentially parasitises magpies (*Pica pica*) and hooded crows (*Corvus corone*) at present (SOLER M. 1990). Indeed, REDONDO & ARIAS DE REYNA (1989) showed that experimentally introduced great spotted cuckoo chicks had similar success in azure-winged magpie and in magpie nests suggesting that azure-winged magpies may be suitable great spotted cuckoo hosts.

The first aim of the present study was to determine whether azure-winged magpies differentiate among threat types. To answer this question we tested the response of azure-winged magpies to three different mounted birds, a predator, the sparrowhawk (*Accipiter nisus*), a female brood parasite, the great spotted cuckoo, and a control, the mistle thrush (*Turdus viscivorus*) at different stages throughout their breeding cycle. We selected the great spotted cuckoo as the target avian brood parasite for our experiment and disregarded the common cuckoo because no evidence of common cuckoo parasitism has ever been reported for the Iberian Peninsula (see above). If azure-winged magpies can differentiate these mounted birds, then we would expect threat specific responses. More specifically, we expect a maximal response to the adult and fledging predator (i.e. sparrowhawk), an intermediate response to the brood parasite and egg and chick predator (i.e. great spotted cuckoo) and a minimal response to the control (i.e. the mistle thrush). Because azure-winged magpies may perceive great spotted cuckoos as a brood parasite, but also as a nest predator, we do not expect a higher level of nest defense against the brood parasite at laying as compared to the nestling phase.

The second aim of this study was to test whether differences in the level of nest defense by azure-winged magpies and magpies may provide a plausible explanation for the current absence of great spotted cuckoo parasitism on Iberian azure-winged magpies. Previous studies have found that the Iberian azure-winged magpie showed a remarkable ability to discriminate and reject great spotted cuckoo eggs (ARIAS DE REYNA & HIDALGO 1982, ARIAS DE REYNA 1998, AVILÉS 2004). In addition, VALENCIA et al. (2005) have argued that the consistent high predation rate suffered by azure-winged magpies across the years may prevent parasitism simply because it is maladaptive for great spotted cuckoos. Alternatively, the current low levels of observed brood parasitism may result from communal defense in the azure-winged magpie (REDONDO & ARIAS DE REYNA 1989, ARIAS DE REYNA 1998), which might induce a high level of defenses, irrespective of the type of threat. We address this last possibility by comparing azure-winged magpie and magpie (the current favorite host for the great spotted cuckoo in Iberia) nest defensive behaviour against a mounted brood parasite. We expected azure-winged magpies to defend more aggressively than magpies.

## METHODS

### *Study species*

The Iberian azure-winged magpie is a flexible cooperative breeder that displays helping at different stages of the breeding cycle (VALENCIA et al. 2003). Azure-winged magpies usually lay five or six eggs (range 2-8) and most first clutches are found in April and the first week of May (J.M. AVILÉS own data). Magpies usually lay six or seven eggs (range 2-10) (SOLER M. et al. 1996), and laying in the study area occurs in March and April (J.M. AVILÉS own data).

Only females of the two species incubate the eggs, starting some days after the first egg is laid (KOMEDA et al. 1987, BIRKHEAD 1991). We have failed to find signs of parasitism by the great spotted cuckoo in the 76 azure-winged magpie breeding attempts studied in our population for this and previous studies, although nearly 15% of magpie *Pica pica* nests in the study area were parasitized (AVILÉS 2004).

### *Study area*

The field study was carried out in the surroundings of Guadiloba reservoir near Cáceres (37°18'N, 3°11'W), southern Spain during March-June 2003-2004. The study area approximately comprised 400 ha in which azure-winged magpies and magpies breed sympatrically with the great spotted cuckoo in a wooded plot of holm oak trees *Quercus ilex* (see AVILÉS 2004 for further details).

### *Experimental procedure*

Azure-winged magpie nests were found by systematically searching appropriate habitats at the beginning of the 2004 breeding season. Once found, nests were monitored every 2 days until they fledged or failed. A total of 24 azure-winged magpie nests were used for this experiment, which represented about the 80% of the nests in the study area. Each pair was tested for nest defense 3 times in a day by alternately presenting taxidermic mounts of a predator, the sparrowhawk, a female brood parasite, the great spotted cuckoo, and a control, the mistle thrush. The sparrowhawk is a common predator in our study area that may potentially eat fledgling and adult azure-winged magpies, although we have no direct evidence for our population. The great spotted cuckoo is a potential brood parasite of the azure-winged magpie, and current evidence would suggest that this parasite used azure-winged magpies in the recent past (AVILÉS 2004). Furthermore, great spotted cuckoos can prey upon host eggs to force acceptance of parasitism (SOLER M. et al. 1995), and the azure-winged magpie may therefore also perceive them as nest predators. The mistle thrush is a regular but uncommon breeder in our area and slightly smaller than the great spotted cuckoo (125 g vs 153 g for a female great spotted cuckoo). While the size of control species should be similar to that of the brood parasite (SEALY et al. 1998), all passerines similar in size to female cuckoos are known to prey on azure-winged magpie nests. In addition, some studies have shown that host responses to control species differing in size were consistent (see review in SEALY et al. 1998). Although the use of several mounts per species is preferable, only one mount was used in this study because the brood parasite and the predator are protected species by the Spanish law. We realize this may affect our results if for instance strangely coloured glass eyes or taxidermist's treatment blocking feather reflectance were used in one mount but not the others. However, mounts were prepared at the University of Extremadura by a single person who used glass eyes exactly resembling the original ones and did not apply any taxidermist treatment to the feathers.

We placed decoys at 0.5 m from the nest at the same height and attached directly to the available vegetation. Mount presentation order was always randomized for different nests and decoys were presented with at least 2 hr between consecutive trials at a single nest. This time interval between two trials is sufficient to prevent carry-over aggression because we noted that azure-winged magpies readily returned to their nests when a trial was finished (see also GILL & SEALY 1996). In addition, we did not present decoys to nests neighbouring any location where we had already made a presentation that day. We tested each nest only once (three trials) from egg laying to chick fledging. Theoretically, if birds discriminate between threats and react optimally, defensive intensity of the azure-winged magpie should peak during the laying in response to parasitism (e.g. GILL & SEALY 1996, SEALY et al. 1998), and during late the nestling period in response to predation (e.g. REDONDO & CARRANZA 1989). Therefore, we randomized our observations throughout the breeding period, and for statistical analyses we

divided the breeding stage of the azure-winged magpie into four discrete categories: 1 = laying, 2 = incubation, 3 = chicks younger than 5 days, and 4 = chicks older than 5 days.

Observations were made approximately 100 m from the nest between 9.00 and 21.00 hr. For analyses we divided the time of day into three discrete periods: (a) morning (9.00 to 13.00 hr); (b) afternoon (13.00 to 17.00 hr) and (c) evening (17.00 to 21.00 hr). The duration of observation was 10 min and it began when the investigator arrived at the observation hide 100 m from the nest after attaching the mount, which was approximately the time when nest owners returned to the nest (i.e. within 10 m of the nest and mount) after researcher disturbance. We consider the decoy as detected if an azure-winged magpie flew within 5 m of the nest during the 10 min observation. After detection, we recorded as measures of the level of aggressiveness: the intensity of the response, number of recruits and response latency. We rated the intensity of response from 1 to 4: 1 is "no reaction" (host was near the nest during the observations but did not pay attention to the decoy, in some cases it even returned to the nest and sat on the eggs); 2 is "alarm calling" (the host performed alarm calls in response to the decoy); 3 is "mobbing" (the host flew around the decoy or dived close to it once or several times, but without touching it); 4 is "attack" (the host vigorously attacked the decoy and touched its body). In the last case the experiment was terminated as soon as the azure-winged magpies started to attack the mount. Sometimes more than one individual responded to the mount during the observation, and we then only recorded the strongest response. Because communal defense of nests has been reported for the azure-winged magpie (REDONDO & ARIAS DE REYNA 1989, ARIAS DE REYNA 1998), we also recorded the number of birds recruited in each trial, and the time in seconds to the strongest reaction after a mount was detected, termed response latency. If the nest owner did not respond (Intensity 1), we arbitrarily recorded the latency as the difference between the detection time and the end of the trial in seconds (any number above the maximum response time would be adequate for the analyses) (GILL et al. 1997).

In 2003, following the same experimental procedure, we also recorded magpie response to the presence of a great spotted cuckoo mount at 26 nests in the same study area. In that case only intensity of response and number of recruits were recorded.

### *Statistical analyses*

We used a generalized linear model (GENMOD procedure; SAS Institute 1996) to test for the association between the probability of decoy detection by azure-winged magpies and decoy type, breeding stage, and time of day. Probability of decoy detection was modeled as a binomial response variable (1 = detection, 0 = no detection) using a logistic link function. Mixed linear models (MIXED procedure in SAS) were used to test the fixed effect of breeding stage, time of day and decoy type on intensity of response, number of recruits and response latency. Nest was introduced in these models as a random effect to account for dependence among trials performed at a single experimental nest. Tukey tests were used to determine the significant differences between group means. Finally, we used two-way ANOVAs (GLM procedure in SAS) to examine whether azure-winged magpies and magpies differ in nest defense intensity and/or number of individuals recruited to defend against a great spotted cuckoo mount. Breeding stages of the azure-winged magpie were recoded for this last analysis as 1 = laying and 2 = the rest of the breeding period, because all magpie expositions were performed before the chicks hatched. We did not include time of day in this analysis because it was not recorded in 2003 (when the magpies were tested). However, this should have a negligible effect on our results because great spotted cuckoo presentations at magpie nests were randomized throughout the day. Starting models contained all the main effects plus all possible interactions except for the analysis of the probability of decoy detection in which we were just able to test main effects. Model selection was carried out by backward elimination.

It should be noted that we treated intensity of nest defense as a quantitative variable, which might affect our conclusions since intensity is a ranked category. Non-parametric statistical techniques do not allow controlling for other factors such as time of day and stage of nesting, which are factors likely to influence the intensity of defense. However, because these

factors proved to be non-significant using parametric approaches (see results) we also analyzed variation in intensity of defense by using non-parametric tests.

## RESULTS

### *Probability of decoy detection*

The chance of detection differed among the types of decoys ( $\chi^2 = 6.41$ ,  $df = 2$ ,  $P = 0.04$ ). Detection of the predator decoy occurred at 100% of the 24 tested pairs, while 88.3% and 75% of those pairs respectively detected the brood parasite and the control decoys. Neither breeding stage ( $\chi^2 = 7.19$ ,  $df = 3$ ,  $P = 0.07$ ), nor time of day ( $\chi^2 = 0.72$ ,  $df = 2$ ,  $P = 0.70$ ) affected the probability of detection. However, the data do not allow us to test for the possible random nest effect due to a null variation of detection probability against the predator decoy. Therefore, because random nest effects are likely to occur (see analyses below), we should consider these results as merely informative.

### *Intensity of response*

After detection, the type of decoy influenced the intensity of response by azure-winged magpies (Table 1). Azure-winged magpies behaved more aggressively against the predator and parasite decoys than against the control (Fig. 1), but the intensity of response was similar when facing a parasite or a predator decoy (Fig. 1). The random effect of nest was significant (Table 1), implying that some pairs always were more aggressive than others. Breeding stage did not determine response intensity as a main effect or as an interaction term. None of the other tested effects significantly affected the intensity of response (Table 1). Our results were qualitative conformed when using non-parametric Friedman ANOVAs in which we could not control for the time of day and the stage of the nesting period ( $\chi^2_2 = 18.14$ ,  $df = 2$ ,  $P < 0.0001$ ). Hence treating intensity as a quantitative variable seemed not to affect our results.

### *Number of recruits*

After detection, the number of recruits depended on the decoy type (Table 1). The number of recruits defending the nest increased from control and parasite to the predator decoy (Fig. 2). However, the number of recruits did not vary when azure-winged magpies were exposed to either the control or the parasite decoy (Fig. 2). The mean number of azure-winged magpies involved in nest defense was around two only when nests were exposed to the predator decoy (Fig. 2). None of the other tested effects was significant in the model (Table 1).

### *Response latency*

Response latency time varied with decoy type (Table 1). Azure-winged magpies responded sooner to the predator and the parasite than to the control decoy (Fig.

Table 1.

Results of the mixed linear models on the effect of decoy type (predator, brood parasite and control), breeding stage (laying, incubation, chicks younger than 5 days and chicks older than 5 days), time of day (9.00 to 13.00 hr, 13.00 to 17.00 hr and 17.00 to 21.00 hr) and nest (as a random effect) on azure-winged magpie nest defense. Nest defense was measured as intensity of response against the decoy (1 = no reaction, 2 = alarm calling, 3 = mobbing and 4 = attack), number of recruits and response latency (see methods). Significant results are in bold type.

Independent effect	Intensity of response	Number of recruits	Response latency
Decoy type	<b>F<sub>2,36</sub> = 9.38, P = 0.0005</b>	<b>F<sub>2,36</sub> = 4.38, P = 0.02</b>	<b>F<sub>2,36</sub> = 10.00, P = 0.0004</b>
Breeding stage	F <sub>3,36</sub> = 0.93, P = 0.43	F <sub>3,36</sub> = 0.65, P = 0.59	F <sub>3,34</sub> = 0.44, P = 0.73
Time of day	F <sub>2,34</sub> = 0.66, P = 0.52	F <sub>2,34</sub> = 0.05, P = 0.95	F <sub>2,34</sub> = 0.78, P = 0.47
Decoy type* Breeding stage	F <sub>6,28</sub> = 1.70, P = 0.16	F <sub>5,25</sub> = 2.24, P = 0.08	F <sub>6,28</sub> = 0.69, P = 0.66
Time of day* Breeding stage	F <sub>5,25</sub> = 0.95, P = 0.47	F <sub>6,28</sub> = 1.90, P = 0.11	F <sub>5,21</sub> = 0.48, P = 0.78
Decoy type* Time of day	F <sub>4,21</sub> = 0.27, P = 0.89	F <sub>4,21</sub> = 2.02, P = 0.13	F <sub>4,24</sub> = 0.79, P = 0.54
Time of day* Breeding stage* Decoy type	F <sub>1,20</sub> = 1.76, P = 0.20	F <sub>1,20</sub> = 3.45, P = 0.08	F <sub>1,20</sub> = 0.13, P = 0.72
Nest	<b>Z = 2.06, P = 0.02</b>	Z = 1.06, P = 0.14	<b>Z = 2.14, P = 0.02</b>

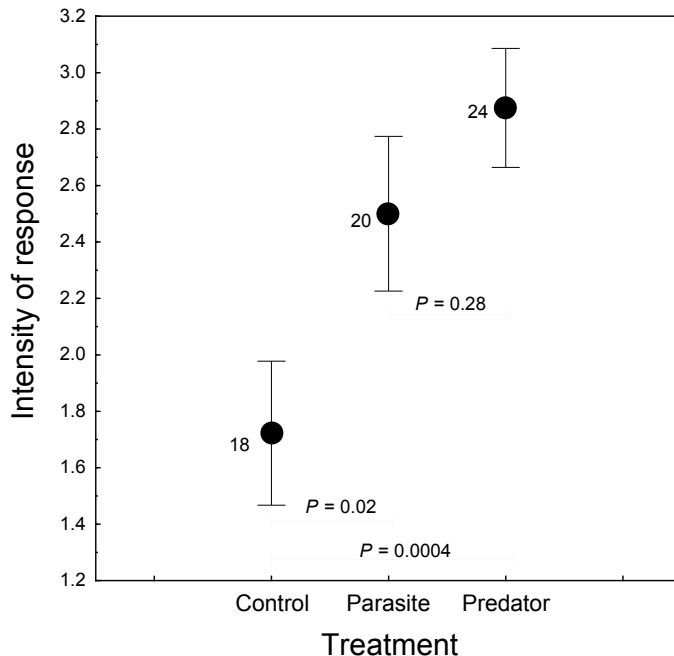


Fig. 1. — Mean ( $\pm$  SE) intensity of response against the different decoy types. Sample size refers to tested nests in which detection of the decoys occurred. Results of post hoc Tukey tests are shown on horizontal lines joining the means under consideration.

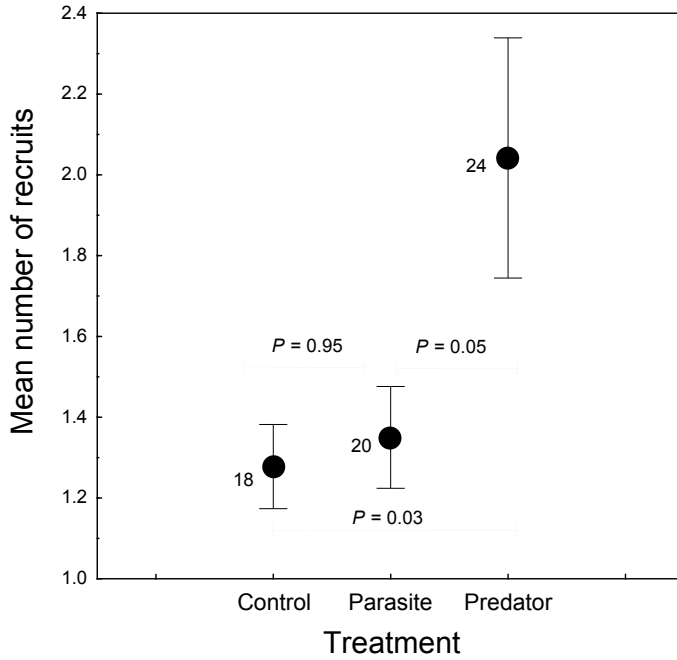


Fig. 2. — Mean ( $\pm$  SE) number of birds recruited for defense in relation the type of decoy. Sample size refers to tested nests in which detection of the decoys occurred. Results of post hoc Tukey tests are shown on horizontal lines joining the means under consideration.

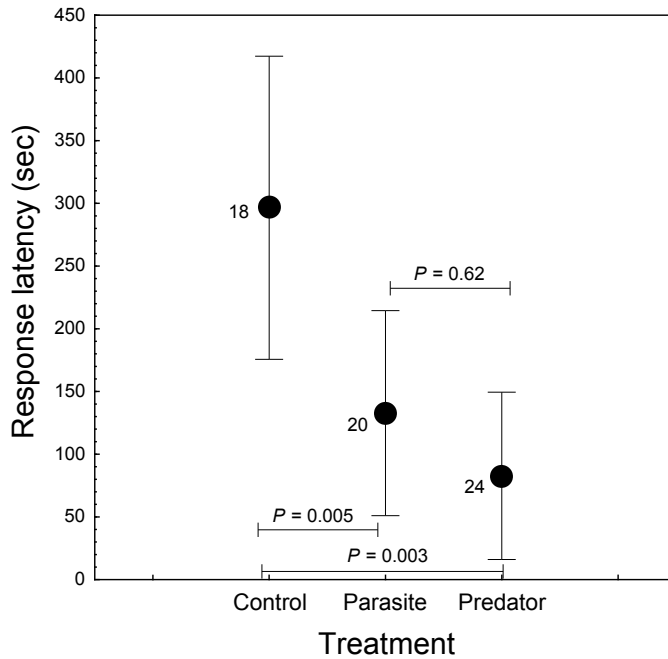


Fig. 3. — Mean ( $\pm$  SE) time of response latency (sec) in relation the type of decoy. Sample size refers to tested nests in which detection of the decoys occurred. Results of post hoc Tukey tests are shown on horizontal lines joining the means under consideration.



3), although response latency time did not vary between the parasite and predator treatments (Fig. 3). This response was not independent of the nest (random effect of nest, Table 1), which suggests that different pairs have different aggressiveness irrespective of stimulus type. No other significant effect was detected for response latency (Table 1).

*Response to parasite decoy by azure-winged magpie and magpie hosts*

The intensity of defense after detection of the brood parasite decoy varied between the azure-winged magpies and the magpies (Two-way ANOVA: species effect,  $F_{1,44} = 4.31$ ,  $P = 0.04$ ). The great spotted cuckoo decoy elicited a stronger response from the azure-winged magpie than from the magpies (mean intensity  $\pm$  SD,  $2.50 \pm 1.27$ ,  $N = 20$  in the azure-winged magpie versus  $1.77 \pm 1.10$ ,  $N = 26$  in the magpie). The breeding stage did not affect the intensity of response to the great spotted cuckoo decoy neither as a main effect (breeding stage effect,  $F_{1,43} = 0.27$ ,  $P = 0.60$ ), nor in an interaction (interaction term,  $F_{1,42} = 0.18$ ,  $P = 0.67$ ). A Mann-Whitney U Test confirmed the differences in intensity between azure-winged magpies and magpies ( $U = 174.00$ ,  $P = 0.05$ ).

In contrast, the number of individuals defending a nest after detecting a great spotted cuckoo decoy did not differ significantly for azure-winged magpies and magpies nests (Two-way ANOVA: species effect,  $F_{1,25} = 0.05$ ,  $P = 0.82$ ; breeding stage effect,  $F_{1,26} = 1.10$ ,  $P = 0.30$ ; interaction term,  $F_{1,24} = 3.23$ ,  $P = 0.08$ ).

## DISCUSSION

Azure-winged magpies discriminated among the different threats as simulated by exposure to three different mounted birds. They behaved more aggressively (i.e. at a higher intensity and with a shorter response latency) when exposed to a great spotted cuckoo and to a sparrowhawk than when they were exposed to a mistle thrush (Figs 1, 3), which suggests that azure-winged magpies discriminate between threat and no-threat. Furthermore, the number of individuals involved in defense was larger when the nests were exposed to a predator than to a mounted control or to a brood parasite (Fig. 2), suggesting that they may also differentiate between different levels of threat. Aggressiveness by the azure-winged magpie towards the mounted great spotted cuckoo was not higher at laying as compared to the other breeding periods, despite the fact that this is the time when the threat of parasitism by the great spotted cuckoo should be at its highest. Therefore, the azure-winged magpie seems to recognize great spotted cuckoos as a threat unrelated to their brood parasitic habits. Finally, azure-winged magpies did not increase their aggressiveness towards the predator in relation to the reproductive value of their offspring suggesting that they did not perceive the sparrowhawk as an egg and/or chick predator, but as a major threat to themselves.

Azure-winged magpies did not perceive great spotted cuckoos as a brood parasite but seemed to recognize it as a threat. SEALY et al. (1998), studying the level of defense shown by hosts of the brown-headed cowbird, found that rejecter species of parasitic eggs responded to a mounted cowbird and control with similar aggressiveness, which was interpreted as a low proneness of rejecters (with low brood para-

site costs) to evolve intense nest defense against a parasite (ROBERTSON & NORMAN 1976, 1977). The azure-winged magpie readily rejects great spotted cuckoo eggs when they are artificially introduced into their nests (ARIAS DE REYNA & HIDALGO 1982, ARIAS DE REYNA 1998, AVILÉS 2004). Consequently, this behaviour would predict a low level of nest defense against the mounted brood parasite according to ROBERTSON & NORMAN'S (1977) hypothesis. However, the azure-winged magpie behaved more aggressively towards the great spotted cuckoo than it did towards the control, suggesting that the parasite was perceived as a threat. Azure-winged magpies may perceive great spotted cuckoos as nest predators. Indeed, previous studies have shown that great-spotted cuckoos can prey upon host eggs but also chicks as a measure of extortion to force acceptance of parasitism (mafia behaviour, SOLER M. et al. 1995). Great spotted cuckoos could be considered by azure-winged magpies as potential predators, which would induce the intermediate response we found. Additional support for this possibility is provided by the absence of breeding phase effects on level of defense against the great spotted cuckoo by the azure-winged magpie. Alternatively, the azure-winged magpie may perceive threat as a function of the size of the mounted bird. Accordingly, we would expect aggressiveness to increase with the size of the mounted bird. This possibility can be ruled out because the intensity and response latency shown by azure-winged magpies did not vary between parasite and predator decoys despite obvious differences in size. Furthermore, the number of recruits attracted to a great spotted cuckoo and a mistle thrush decoy did not vary. In addition, previous studies have reported a consistent response towards control mounted birds independent of their size, which would suggest that size is unimportant (e.g. DUCKWORTH 1991, GILL & SEALY 1996, SEALY et al. 1998).

Azure-winged magpies seemed to perceive the predator as the major threat irrespective of the breeding stage. This finding may be the consequence of the predatory characteristics of the species we used as predator. The sparrowhawk could be regarded by azure-winged magpies as an adult predator more than than a chick or egg predator, which diminishes the importance of nest reproductive value as a factor inducing nest defense. Previous studies reporting a seasonal increase in the level of defense against a mounted predator preferentially used an egg and/or chick predator (GILL & SEALY 1996, SEALY et al. 1998). However, this seems not to be a prerequisite because several studies have shown a consistent increase in the level of defense against predators as the reproductive offspring value increases when using mounts of predator species that preying on both adults and offspring (e.g. PAVEL & BUREŠ 2001, RYTKÖNEN 2002). Alternatively, it could be argued that we may be unable to detect whether nest owners are defending the nest according to its reproductive value because of the communal defense shown by the azure-winged magpie. This seems unlikely because the mean number of recruits at the nests was about two individuals only when exposed to a mounted predator (Fig. 2).

Our results imply that azure-winged magpies defended more intensely than magpies when they face a mounted great-spotted cuckoo, although the number of birds attacking the decoy was similar for both species. Therefore, the defensive behaviour of azure-winged magpies could be one of the key factors explaining the current absence of parasitism by the great spotted cuckoo in Iberia. Indeed, magpies show a lower intensity of defensive behaviour against the parasite than did the azure-winged magpies despite the fact that the former is the primary host. It should be noted that azure-winged magpies defended their nest from the great spotted cuckoo at a higher intensity than do magpies even though they apparently do not

recognize the threat of brood parasitism (this study). Consequently, azure-winged magpies show a high non-specific level of defense that might be modulated by factors other than brood parasitism, such as nest predation. Indeed, Iberian azure-winged magpies have extremely high predation rates with up to 80% of their nests lost in a single season (CRUZ et al. 1990). Hence, nest predation is likely to be a factor that explains the high willingness to defend their nests irrespective of brood parasitism. Finally, our data did not allow us to conclude that the existence of communal defense by the azure-winged magpie was the mechanism preventing great spotted cuckoo parasitism. In fact, we failed to find differences in the number of individuals recruited for defense in magpie and azure-winged magpie nests.

In conclusion, our results suggest that the azure-winged magpie is able to discriminate among different threats during the breeding season and to respond differently to them. They responded most aggressively towards a potential predator. Although they are potential suitable hosts for the great spotted cuckoo, and the current evidence suggests that they were widely used as hosts in the recent past, they do not seem to recognize the great spotted cuckoo as a brood parasite but as an egg and chick predator. Furthermore, the high willingness of azure-winged magpies to defend their nests could be a consequence of the high level of nest predation suffered by the species in the region and this in turn could lead to prevention of parasitism by the great spotted cuckoo.

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