

# Winter male plumage coloration correlates with breeding status in a cooperative breeding species

Elena Solís,<sup>a</sup> Jesús M. Avilés,<sup>b</sup> Carlos De La Cruz,<sup>a</sup> Juliana Valencia,<sup>c</sup> and Gabriele Sorci<sup>d</sup>

<sup>a</sup>Departamento de Biología Animal, Facultad de Ciencias, Universidad de Extremadura, 06071 Badajoz, Spain, <sup>b</sup>Departamento de Biología Animal y Ecología, Facultad de Ciencias, Universidad de Granada, E-18071 Granada, Spain, <sup>c</sup>Cátedra de Biología y Etología, Facultad de Veterinaria, Universidad de Extremadura, 10071 Cáceres, Spain, and <sup>d</sup>BioGeosciences, CNRS UMR 5561, Université de Bourgogne, 6 Boulevard Gabriel, 21000 Dijon, France

The function of colored ornaments is usually related to the signaling of individual quality in intra- and intersexual interactions. In cooperative breeding species, where only a fraction of the male population access the breeding status and the other fraction has the option to help breeding pairs, colored traits might provide the females with a reliable information on the quality of potential mate. Males of the cooperative breeding azure-winged magpies (*Cyanopica cyanus*) display conspicuous blue plumage coloration. Here we explored the role played by structural blue coloration of males and the probability of becoming a breeder or a helper. Birds were trapped during 4 consecutive years, and feather coloration was measured with a spectrometer. Males that became breeders had a more brilliant and saturated blue coloration and showed a more violet hue in the nonbreeding period compared with birds that became helpers. Breeding males also showed a seasonal decline in blueness, whereas the color properties of helpers were constant throughout the year. Blueness of individuals trapped in the nonbreeding period was positively correlated with body size and condition. These findings are consistent with a scenario in which nonbreeding blue plumage coloration may function as a signal of individual quality in the azure-winged magpie at the pair formation time and add to growing evidence suggesting that the nonbreeding season appears particularly important in impacting breeding roles in cooperative breeding birds. *Key words:* cooperative breeding, *Cyanopica cyanus*, nonbreeding plumage, sexual selection, structural coloration. [*Behav Ecol* 19:391–397 (2008)]

Sexual selection explains the evolution of extravagant male ornaments in many species, such as plumage colors, and elaborate visual or vocal displays on the basis of differences in breeding success caused by competition over mates (Darwin 1871). Some empirical evidence suggests that elaborated ornamental traits may be costly to produce or maintain and, thereby, that only individuals of the highest quality can achieve maximum expression of such traits (Zahavi 1975; Kodric-Brown and Brown 1984; Andersson 1994). Therefore, male ornaments may function as honest signals of bearer quality to possible mates and/or competitors (Kodric-Brown and Brown 1984). The role of colored signals in the process of mate choice has been extensively shown in a huge diversity of organisms including both invertebrates and vertebrates (Andersson 1994).

In cooperatively breeding species, only a fraction of the population engage in reproduction, whereas nonbreeding individuals assist breeding pairs in caring the offspring (Brown 1987). The evolutionary costs and benefits of helping behavior have attracted considerable attention in the last decades, with emphasis put on the inclusive fitness benefit of this apparently altruistic behavior (Griffin et al. 2005; Young et al. 2007). The suite of proximal ontogenic cues that determine whether a given individual will become a breeder or a helper is also a major focus of current research on cooperative breeding (Cockburn 1998). Plumage polymorphism may be obviously

a good candidate for such determinism. Species who have helpers recruited among young immature males may have a delayed acquisition of breeding plumage that could serve as a signal of nonbreeding status (Beauchamp 2003). However, in other species, adult plumage is acquired during the first moult, and any effect of plumage color on the likelihood to become a breeder is therefore due to more subtle effect of color signaling individual quality. To our knowledge, this effect of interindividual variation in adult plumage color on the breeding status has not been investigated yet.

The azure-winged magpie (*Cyanopica cyanus*) is a small colonial corvid (Cramp and Perrins 1994), with a cooperative socially monogamous breeding system (Hosono 1983; Komeda et al. 1987; Valencia et al. 2003). Helpers are those individuals that collaborate with the breeding pair in feeding the offspring and removing the fecal sacs from the nest (Komeda et al. 1987). Azure-winged magpies can behave as helpers either as a first option or after having attempted their own breeding—so-called second-option helpers (Valencia et al. 2003). First-option helpers are always males, whereas most of second-option helpers were males too (only 9 females were reported as helpers after losing their own breeding in 15 years; De La Cruz C, Solís E, Valencia J, unpublished data), and first-year magpies are more likely to help than older birds (Valencia et al. 2003). Males and females of this species exhibit colorful blue wing and tail feathers all year around (Avilés et al. 2008). Suggesting a signaling function of this coloration, blue coloration is particularly conspicuous during encounters with other individuals due to an energetic tail movements and a typical sloping wing behavior that emphasizes the upper wing blue parts (Cramp and Perrins 1994). Azure-winged magpies form

Address correspondence to J.M. Avilés. E-mail: javiles@eeza.csic.es.

Received 21 February 2007; revised 27 November 2007; accepted 27 November 2007.

foraging flocks out of the breeding season (Cramp and Perrins 1994; Cruz 2004) in which dominance status relationships are established (De La Cruz C, Solís E, Valencia J, personal observation). Also, preliminary analyses have shown that winter translocated magpies, coming from distant localities and released at our study population, did not flock with the native birds, showing that azure-winged magpie have the potential to discriminate conspecifics on the basis of some phenotypic traits (Solís E, De La Cruz C, Valencia J, unpublished data). There is not evidence of assortative mating with respect to structural blue coloration in azure-winged magpies (Avilés et al. 2008). Also, the facts 1) that all females but not all the males reproduce irrespective of age, 2) that adult sex ratio is biased to males in our population, 3) that the highest predation during the reproduction is suffered by females (Cruz 2004), and 4) that nest predation decreases with plumage brightness of males (Avilés et al. 2008) would suggest that females would be more likely the choosy sex in this species (e.g., Double and Cockburn 2003; Rubenstein 2007a).

In this study, we tested whether structural blue coloration is related to reproductive status (breeder vs. helper) in male azure-winged magpies. Recent findings have shown that plumage coloration may potentially be used to assess parental qualities by potential mates in both sexes of the azure-winged magpie because blueness negatively correlated with probability of nest predation in this species (Avilés et al. 2008). These findings add to growing evidence in other species that 1) full expression of structural coloration requires a good condition through the moult period (e.g., Keyser and Hill 1999, 2000; Doucet 2002; McGraw et al. 2002; Doucet and Montgomerie 2003; Siefferman and Hill 2003, 2005a, 2005b) and 2) the expression of structural plumage coloration serves as a signal in male–male interactions (Alonso-Álvarez et al. 2004; Siefferman and Hill 2005a) and during female's mate choice decisions (Andersson and Amundsen 1997; Bennett et al. 1997; Johnsen et al. 1998).

Here, we specifically tested 3 predictions related with the signaling function of blue coloration as a determinant of breeding status in azure-winged magpies. Recent findings provide support for the view that maintenance of feather colorations might be costly and, thereby, that changes in plumage coloration after the moult period may differ as function of individual quality (Örnborg et al. 2002; Delhey et al. 2006). Breeders and helpers greatly differ in their reproductive investment (see Valencia et al. 2003, 2006), which leads us to predict that seasonal changes in male azure-winged magpie blueness should correlate with the reproductive status (Prediction 1). In addition, we expect postmolt (nonbreeding) plumage blueness to be a better predictor of individual quality than spring plumage coloration (Prediction 2). Finally, because studies with other species have shown that only individuals of the highest quality can achieve maximum expression of blueness (e.g., McGraw et al. 2002), we expect that individuals displaying a bluer postmolt plumage should have higher chances to become breeders, whereas males with duller postmolt plumage should have higher chances to become helpers (Prediction 3).

## MATERIALS AND METHODS

### Study site and data collection

The study was carried out in a colony of Iberian azure-winged magpies 22 km north of the city of Badajoz (39°03' N, 6°48' W) in the middle of the species' Iberian distribution (Sacarrao 1967) during 4 consecutive years (2002–2005). The predominant habitat is the dehesa (open holm oak *Quercus ilex* woodland), and the climate is typically Mediterranean, with dry hot summers and mild wet winters (Valencia et al. 2003, 2006).

Birds were captured from October to July (October, 4 birds; November, 8 birds; December, 2 birds; January, 5 birds; February, 16 birds; March, 16 birds; April, 9 birds; May, 17 birds; June, 6 birds; July, 1 bird), using a specially designed trap (see details in Valencia et al. 2006) and marked with a metal ring and 1 unique combination of color plastic rings that allowed individual recognition. On capture, we measured tarsus length using a digital calliper to the nearest 0.01 mm and weighted birds using a Pesola balance of 0.5 g of precision. Wing chord and tail length were measured with a rule to the nearest 1 mm. Sex of breeders was assessed during the breeding season by focal observation of individuals' behavior (only females incubate the eggs and brood the young in this species, Cramp and Perrins 1994; Cruz 2004). Helpers usually joined the breeding group after the chicks hatched, and only sporadically during the laying period, but never at the beginning of the laying. This allowed us to always distinguish breeding and helping males (Valencia et al. 2006). Because we were particularly interested in knowing if it was necessary to achieve a particular plumage coloration to become a breeder in this species (see Introduction), here we will exclusively focus on first-option helpers that are invariably males (De La Cruz C, Solís E, Valencia J, unpublished data). Nonetheless, to definitively discard sexual discrimination errors, sex of all sampled individuals was corroborated by reports of breeding behavior in different breeding seasons as well as by genetic analyses. Age was assigned using moult extension, following Cruz et al. (1992) as: juveniles, individuals that had completed the first partial postjuvenile moult but had not yet undergone the postnuptial moult, and adults, birds older than 1 year that had completed the postnuptial moult. A total of 84 males comprising 65 breeders (53 adults and 12 juveniles) and 19 helpers (6 adults and 13 juveniles) were captured and classified with this method. Although few birds were recaptured between years, we only used data for the first capture in the statistical analyses to avoid pseudoreplication.

### Plumage color

On capture, we collected 2 secondary wing covert feathers from each individual for spectrometric plumage analysis. Moult can extend from May in adults and July in juveniles to early November (Cruz et al. 1991, 1992). Secondary wing coverts were moulted in adults and juveniles at the time of capture. Feather samples were carefully plucked from the same location on all birds. At the time of data color collection, feathers were carefully placed on black paper in a fashion that mimicked the way the feathers naturally lay on the bird. We quantified plumage reflectance in the range 300–700 nm with a spectrometer with a deuterium and a halogen light source (DH 2000, Ocean Optics Europe, Eerbeek, The Netherlands) using a bifurcated micron fibre optic probe at a 45° angle from the feather surface and illuminating an area of 1 mm<sup>2</sup>. Using OOIBase, a spectra acquisition software package, we sequentially recorded 10 spectra relative to a standard white reference (WS-2) and then averaged the spectra to reduce electrical noise from the collection array within the spectrometer. This process was repeated 3 times; the probe lifted and replaced on the feathers at each scan. We then averaged the 3 spectra for each individual.

In a previous work, it is shown that wing covert feathers of azure-winged magpie males and females reflect most strongly in the violet and the blue region of the spectrum (Avilés et al. 2008). We summarized reflectance data by calculating 3 different standard descriptors of reflectance spectra: brightness, hue, and chroma. Brightness, or total amount of light reflected by the feather, is the summed reflectance over the 300–700 nm range (e.g., Siefferman and Hill 2005b). Hue corresponds to the wavelength at which the maximum pick

of reflectance is reached within the ultraviolet–blue waveband (300–500 nm). Chroma (spectral purity) is the ratio between the spectral reflectance in the ultraviolet–blue waveband (300–500 nm) and the reflectance of the entire spectrum (300–700 nm) (Siefferman and Hill 2003). Color variables were then entered into a principal component analysis (PCA) to yield a single color score (principal component 1 [PC1]) that was then used in all the analysis (e.g., Doucet and Montgomerie 2003; Jawor et al. 2004). The first principal component (PC1) from this analysis explained 48.20% of the variation in color. Total brightness and ultraviolet–blue chroma loaded negatively, whereas hue loaded positively (eigenvalues =  $-0.67$ ,  $-0.60$ , and  $0.79$ , respectively). Therefore, individuals with a high positive PC1 color score displayed an overall less bright and saturated structural plumage coloration and showed a peak of maximum reflectance at a higher wavelength than individuals with negative PC1 color scores.

Structural plumage coloration is not a static trait, and changes in coloration can occur after moulting (e.g., Örnborg et al. 2002; Tubaro et al. 2005; Delhey et al. 2006; Shawkey et al. 2007). To account for this potential seasonal variation, we classified feathers in relation to the period in which they were collected as “freshly” moulted feathers, when collected from birds captured from October to February (nonbreeding period), and “late” moulted feathers, when collected from birds trapped from March onward. This classification clearly makes sense because structural color varies significantly between these 2 periods in azure-winged magpies. Feathers collected from birds captured from October to February have more brilliant and saturated blue coloration and show a more violet hue than those collected afterward (Avilés et al. 2008). In addition, the earliest clutches reported in our population were from the last part of March (average laying date = 2 April, Cruz 2004). Therefore, period was included in all the statistical analyses as a fixed factor to account for this seasonal effect.

### Body size and condition

Morphological variables (wing chord length, tail length, and tarsus length) were entered into a PCA to yield a single body size score (PC1). The first principal component (PC1) from this analysis explained 54.34% of the variation in size, and it was subsequently used as index of body size. Wing chord length, tail length, and tarsus length loaded negatively (eigenvalues =  $-0.82$ ,  $-0.70$ , and  $-0.69$ , respectively). Therefore, individuals with a high positive PC1 score were smaller in size than individuals with high negative scores.

Residuals of body mass on body size PC1 scores and on date of capture were used as an index of body condition. Including date of capture allowed us to control for possible seasonal changes in body condition.

### Statistical analysis

We used a generalized linear mixed models (GLMMs) in which year was included as a random factor (link function: identity, PROC MIXED, SAS Institute, 1996) to test for the association between structural coloration (PC1 scores from structural plumage coloration), breeding status, and individual quality (body size and body condition index). Age and season were entered as fixed factors in the model to control their possible effect on plumage colouration. The hypothesis under evaluation hinges on the status by season interaction (Prediction 1), which tests whether changes in coloration between periods are parallel for breeders and helpers. Therefore, 2-way interactions terms were also entered in the saturated model. Model selection was carried out by removing, one by one, the effects that were the furthest from statis-

**Table 1**  
GLMM analyzing determinants of blue coloration in male azure-winged magpies

Independent effect	df	F/Wald-Z	P
Excluded terms			
Body condition × status	1,64	0.00	0.99
Body size × status	1,65	0.10	0.75
Age × status	1,66	2.76	0.10
Age	1,70	0.18	0.67
Body condition	1,67	0.05	0.82
Body size	1,71	1.42	0.23
Included terms			
Period	1,80	0.49	0.49
Status	1,80	1.66	0.20
<b>Period × status</b>	<b>1,80</b>	<b>6.38</b>	<b>0.01</b>
Year		0.12	0.45

Independent effects are ordered as they were removed (see Materials and Methods). Significant effects are reported in bold. Analysis based on 84 birds trapped during 4 consecutive years. Four birds were not sampled for body size and condition due to logistic problems.

tical significance (0.05), starting with the highest order interactions down to the main effects. *t*-Tests for independent samples were used to separately explore seasonal differences in azure-winged magpie coloration of breeders and helpers and differences in the date of capture of breeding birds and helpers within the nonbreeding season.

In a second set of analyses, we tested the association between PC1 color scores and body size, condition and/or age (Prediction 2), using GLMM in which year was included as a random factor (link function: identity, PROC MIXED, SAS Institute, 1996). Body size and condition were not significantly related in our sample of birds ( $r_p = -0.18$ ,  $P = 0.11$ ,  $N = 76$  birds), which made collinearity unlikely.

Finally, we used a GLMM for binary dependent variables (link function: logit, SAS Macro program GLIMMIX, SAS Institute, 1996) to test the effect of age, body size, condition, and/or color as predictors of the probability of being a breeder or a helper (Prediction 3). Year was entered as a random factor in this model. The best-fit model for analyses based on nonbreeding birds (Predictions 2 and 3) was determined using Akaike's information criterion (AIC) as an estimate of the improvement in fit for addition of variables (Burnham and Anderson 2002). Because the number of data points in the model divided by  $K$  (the number of parameters in the model) is less than 40, AIC was corrected for small sample sizes (known as AICc) following Burnham and Anderson (2002). The model with the lowest value of AICc is the most parsimonious one in the sense that it provides the best balance between overfitting (hence loss of precision) and underfitting (hence bias) and is the selected model. The Akaike weights give the relative support that a given model has from the data compared with the other models in the set (all information in Burnham and Anderson 2002).

Sample sizes differ for some analyses because we could not measure all the variables for a few individuals.

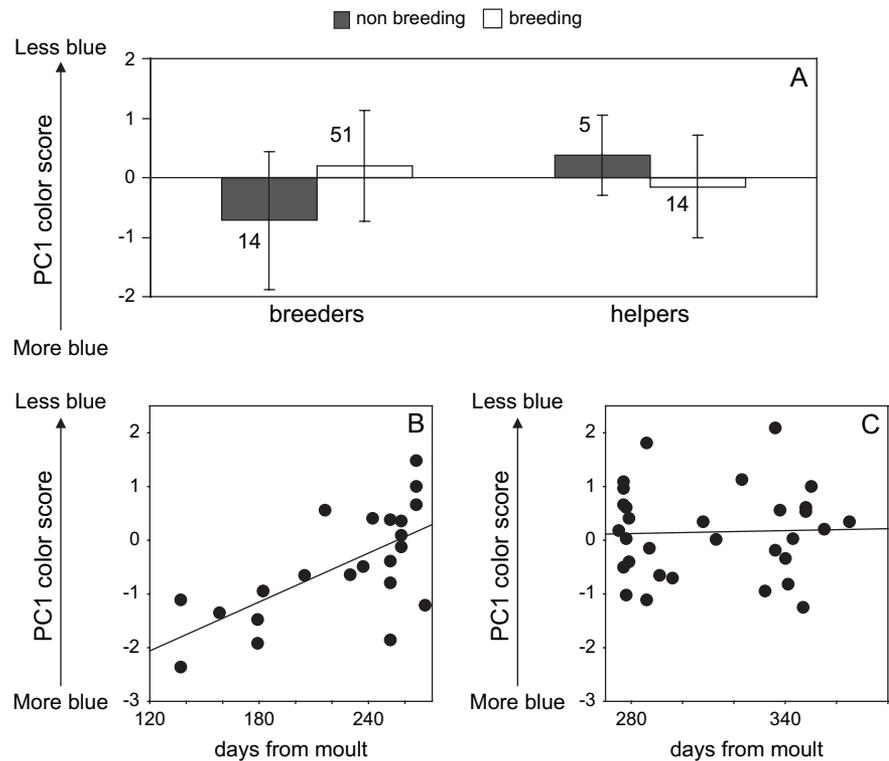
## RESULTS

### Prediction 1: does seasonal variation in blueness differ with male reproductive status?

Blueness changed seasonally in a different way for breeders and helpers (Table 1). Breeders have more brilliant and saturated blue coloration and showed a more violet hue (i.e., lower PC1 scores) during the nonbreeding period than during the

**Figure 1**

Seasonal variation in average ( $\pm$ standard deviation) blueness of male azure-winged magpies in relation to reproductive status (breeder vs. helper) (A), and variation of blueness of breeders in relation to date from moult (see Materials and Methods) for the nonbreeding (B) and breeding (C) periods, respectively. PC1 scores came from a PCA combining 3 spectral characteristics of azure-winged magpie coloration: individuals with a high positive PC1 color score displayed and overall less bright and saturated structural plumage coloration and showed a peak of maximum reflectance at a higher wavelength than individuals with negative PC1 color scores (see Materials and Methods). Sample sizes are displayed close to the mean value. Lines in (B) and (C) represent the best fit of a simple linear regression between PC1 color scores and days from moult.



breeding period ( $t$ -test,  $t_{63} = 3.11$ ,  $P = 0.003$ , Figure 1A). A closer look to the seasonal change in blueness of breeders revealed that the loss of coloration mostly occurred during the nonbreeding period (Figure 1B) and that once reproduction has started coloration remained invariable (Figure 1C). Differences were not due helper and breeding birds being captured at different times within the nonbreeding season ( $t$ -test,  $t_{17} = 1.00$ ,  $P = 0.32$ ). Blueness of helpers, however, did not significantly vary between the 2 periods ( $t$ -test,  $t_{17} = -1.22$ ,  $P = 0.24$ ). Age, body condition, and body size did not contribute to explain blueness either as main effects or in interaction with status (Table 1). Blueness did not vary among study years (Table 1).

### Prediction 2: does nonbreeding blueness predict male quality?

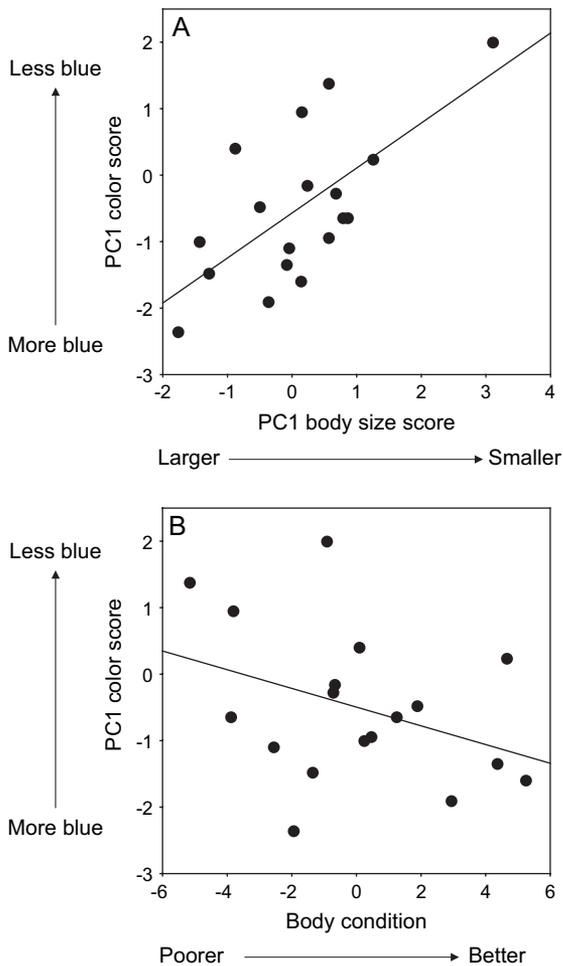
When we restricted our analysis to the nonbreeding period, the most parsimonious model explaining magpie male blueness included body size, body condition, and the random effect of year (Table 2, Prediction 2). Adding age to that model or considering solely body condition or body size with year did not improve the models (Table 2). Therefore, male body size (GLMM:  $F_{1,13} = 15.30$ ,  $P = 0.002$ , Figure 2A) and body condition (GLMM:  $F_{1,13} = 4.67$ ,  $P = 0.049$ , Figure 2B) were significantly correlated with blueness once we controlled for year (GLMM: year effect:  $Z = 0.04$ ,  $P = 0.48$ ). Male magpies with larger body size and a better body condition displayed

**Table 2**

The table shows a summary of the model selection for the analysis of Predictions 2 and 3

Model	Factors	<i>K</i>	Deviance	AICc	Delta AICc	Akaike weight
Prediction 2: blueness predicts male quality						
1	Body size, body condition, age, year	6	7.46	56.24	2.24	0.28
2	<b>Body size, body condition, year</b>	<b>5</b>	<b>9.68</b>	<b>54.00</b>	<b>0.00</b>	<b>0.84</b>
3	Body size, age, year	5	10.88	54.50	0.50	0.66
4	Body condition, age, year	5	12.41	59.80	5.80	0.05
Prediction 3: blueness predicts breeding status						
1	Color, age, year	5	16.18	31.18	3.28	0.11
2	Color, body size, year	5	15.66	30.66	2.76	0.15
3	Color, body condition, year	5	15.65	30.65	2.75	0.15
4	<b>Color, year</b>	<b>4</b>	<b>16.80</b>	<b>27.88</b>	<b>-0.02</b>	<b>0.59</b>

The table shows the factors included in the model. Model selection was based on AICc, and delta AICc is the difference between a particular model and the best one within each subanalysis (in bold). *K* is the number of estimated parameters. Deviance is the difference in log-likelihood between the current and the saturated model, the latter being a model with number of parameters equal to the sample size. Akaike weights show the relative support a given model has from the data compared with the other models in the set. Analyses based on 19 birds trapped during 4 consecutive years in the nonbreeding period.



**Figure 2**  
Relationships between winter male blueness (PC1 color scores) and (A) body size (PC1 scores of a PCA on 3 morphological variables [see Materials and Methods] and (B) body condition (residuals of body mass on PC1 scores summarizing body size and date of capture). Displayed values are raw data.

brighter, more saturated blue colorations and less green-biased hues during the nonbreeding period (Figure 2A,B).

### Prediction 3: does nonbreeding blueness predict probability of breeding versus helping?

The most parsimonious model explaining probability of becoming a helper included PC1 color scores and the random effect of year (Table 2, Prediction 3). Models in which age, body size, or body condition were added to that model had considerably lower Akaike weights (Table 2). PC1 color scores were significantly correlated with the probability of becoming a breeder (GLMM:  $F_{1,15} = 10.97$ ,  $P = 0.005$ ) once we control for the random effect of year (GLMM: year effect:  $Z = 0.29$ ,  $P = 0.38$ ). Breeders showed a more brilliant and saturated blue coloration and a more violet hue than helpers during the nonbreeding period (Figure 1).

## DISCUSSION

Our results reveal the existence of seasonal changes in blue plumage coloration of male azure-winged magpies that depend on the reproductive status. Breeders' blueness varied from the nonbreeding period to spring, whereas it did not

vary for helpers. Specifically, breeders' plumage become less brilliant and with a less saturated violet–blue coloration and a greener hue in spring. In addition, blueness of individuals trapped in the nonbreeding period was correlated with body size and condition. Furthermore, blueness of individuals sampled in the nonbreeding period predicted the probability of becoming a breeder or a helper in the following breeding attempt. Bluer individuals were larger and had a better condition and were more likely to become breeders in the spring, whereas dull blue-colored males mostly became helpers. To our knowledge, this is the first study linking plumage coloration and reproductive status for a cooperative breeding bird.

### Seasonal change in blueness depends on reproductive status

Males that acted as breeders displayed a more brilliant and saturated blue color with a more violet hue in nonbreeding period than in spring, whereas we did not report detectable changes in blue coloration of helpers from nonbreeding period to spring. Several mutually nonexclusive mechanisms may explain the differential pattern of change in coloration for breeders and helpers. It could be argued that helpers were incapable of producing the bluest coloration during the nonbreeding season, whereas breeders are able to pay the production cost of better feathers during molt. Supporting this view, feather blueness at capture was correlated with body size and condition during the nonbreeding season. Alternatively, seasonal changes in Azure-winged magpie blue coloration could be due to the differential action of feather wear for breeders and helpers (Örnberg et al. 2002; Tubaro et al. 2005; Delhey et al. 2006). Indeed, wear has been hypothesized to have especially strong effects on structurally colored feathers (Fitzpatrick 1998). In addition, the progressive accumulation of dirt and fat on the feathers might be responsible for the decline in UV reflectance because these substances often absorb UV light (Örnberg et al. 2002; Zampiga et al. 2004). Also, ectoparasites (Kose and Møller 1999) and bacteria (Shawkey et al. 2007) may affect plumage coloration by damaging feathers or some of their parts. Preening is the mechanism that serves the purpose of cleaning by removing dirt and parasites, arranging and generally maintaining the plumage. Moreover, the degree of investment in feather maintenance would prevent or diminish the effect of wearing (Zampiga et al. 2004). Birds devote a substantial part of their daily time budget to feather maintenance activities (Cotgreave and Clayton 1994) that may result in a temporal trade-off between investment in plumage maintenance and other activities, such as foraging or vigilance (Redpath 1988; Christe et al. 1996; Cucco and Malacarne 1997). However, it does not seem that breeders are differentially maintaining their color throughout the year compared with helpers because helpers never had a deep blue color during the winter and the change in coloration of breeders mostly occurred during the nonbreeding season (Figure 1). However, although we intensively trapped birds during 4 consecutive years, only a few individuals were trapped twice in a single season, which precluded analyses based on longitudinal data. Therefore, we cannot exclude that differential mortality or emigration associated with bird coloration could have generated the observed results.

### Nonbreeding blueness predict male quality and probability of breeding

Male blueness of individuals trapped during the nonbreeding period covaried positively with body size and body condition at that time (Figure 2). In turn, breeder males showed a more brilliant and saturated blue coloration and a more violet hue than helpers during that time irrespective of their age. These

results suggest that blue coloration is a condition-dependent trait during the nonbreeding season and may have the potential to reveal male quality in azure-winged magpies. Although we do not know exactly when pair formation occurs in azure-winged magpies, it seems reasonable to assume that it should be somewhere within the nonbreeding season (i.e., from October to February). This suspicion is based on the evidence that azure-winged magpies forms flocks in the nonbreeding period composed by the same individuals that will later reproduce in the colony (De La Cruz C, Solís E, Valencia J, unpublished data). Furthermore, there exists evidence of the existence of dominance status in these flocks in food-supplemented situations (De La Cruz C, Solís E, Valencia J, unpublished data). However, we did not detect signs of aggression during our observations, which suggests that individual recognition (which is facilitated by long-term permanence of individuals in closed flocks) may function as the mechanism leading to dominance status. Thus, individual evaluation based on plumage coloration could be passively made at any time within the nonbreeding period. Finally, the fact that plumage coloration reveals aspects of individual condition during the nonbreeding period but not later would support this view. Our findings are in agreement with a number of studies, suggesting that structural coloration has the potential to function as a condition indicator trait (e.g., Keyser and Hill 1999, 2000; Doucet 2002; Doucet and Montgomerie 2003; Siefman and Hill 2003, 2005a, 2005b). Mate formation occurs in winter for some bird species (e.g., Bronson et al. 2003; Woodcock et al. 2005), and females may discriminate the quality of potential mates by using plumage characteristics (Woodcock et al. 2005) or social rank (dominance) (Bronson et al. 2003).

In conclusion, based on a cross-sectional approach, we have found that structural blue coloration in azure-winged magpie males changed seasonally in breeders but not in helpers. Furthermore, our findings suggest that nonbreeding but not spring blue plumage coloration has the potential to reveal male quality and the probability to become a breeder. Therefore, blue plumage coloration may play a previously ignored role in the assessment of mate quality during nonbreeding when azure-winged magpie form flocks. These findings add to growing evidence, suggesting that for cooperative breeding birds the nonbreeding season appears especially important in affecting subsequent breeding roles and dispersal decisions (e.g., Dickinson and McGowan 2005; Rubenstein 2007b) and may suggest that helping in the azure-winged magpie is a suboptimal strategy because it is adopted by individuals that cannot reach the minimum threshold for reproduction.

## FUNDING

Junta de Extremadura project (2PR02A080 to C.C.). Autonomous Government of Extremadura and an I3P contract from the European Union, respectively, to E.S. and J.M.A.

We are grateful to M.A. Pitarch and the Valdesequera's staff for permission and facilities, as well as to all people who collaborated at different stages of fieldwork. We also thank D. Parejo and J.J. Soler for helpful discussions.

## REFERENCES

- Alonso-Álvarez C, Doutrelant C, Sorci G. 2004. Ultraviolet reflectance affects male-male interactions in the blue tit (*Parus caeruleus ultramarinus*). *Behav Ecol*. 15:805–809.
- Andersson M. 1994. *Sexual selection*. Princeton (NJ): Princeton University Press.
- Andersson S, Amundsen T. 1997. Ultraviolet colour vision and ornamentation in bluethroats. *Proc R Soc Lond B Biol Sci*. 264:1587–1591.
- Avilés JM, Solís E, Valencia J, Cruz C, Sorci G. Forthcoming 2008. Female and male plumage brightness correlate with nesting failure in azure-winged magpies. *J Avian Biol*.
- Beauchamp G. 2003. Delayed maturation in birds in relation to social foraging and breeding competition. *Evol Ecol Res*. 5:589–596.
- Bennett ATD, Cuthill IC, Partridge JC, Lunau K. 1997. Ultraviolet plumage colors predict mate preferences in starlings. *Proc Natl Acad Sci USA*. 94:8618–8621.
- Bronson CL, Grubb TC, Sattler GD, Braun MJ. 2003. Mate preference: a possible causal mechanism for a moving hybrid zone. *Anim Behav*. 65:489–500.
- Brown JL. 1987. *Helping and communal breeding in birds: ecology and evolution*. Princeton (NJ): Princeton University Press.
- Burnham KP, Anderson DR. 2002. *Model selection and multimodel inference*. New York: Springer.
- Christe P, Richner H, Oppliger A. 1996. Of great tits and fleas: sleep baby sleep. *Anim Behav*. 52:1087–1092.
- Cockburn A. 1998. Evolution of helping behavior in cooperatively breeding birds. *Ann Rev Ecol Syst*. 29:141–177.
- Cotgreave P, Clayton DH. 1994. Comparative analysis of time spent grooming by birds in relation to parasite load. *Behaviour*. 131:171–187.
- Cramp S, Perrins CM, editors. 1994. *Birds of the western Palearctic*. Vol. 8. Oxford: Oxford University Press.
- Cruz C. 2004. Rabilargo (*Cyanopica cyanus*). In: Carrascal LM, Salvador A, editors. *Enciclopedia virtual de los vertebrados de españoles*. Madrid (Spain): Museo Nacional de Ciencias Naturales. Available from: URL <http://www.vertebradosibericos.org/>.
- Cruz C, de Lope F, da Silva E. 1991. La muda postnupcial en el rabilargo (*Cyanopica cyanus cooki*). *Ardeola*. 38:101–115.
- Cruz C, de Lope F, Sánchez JM. 1992. Postjuvenile moult in the azure-winged magpie *Cyanopica cyanea cooki*. *Ringing Migr*. 13:27–35.
- Cucco M, Malacarne G. 1997. The effect of supplemental food on time budget and body condition in the Black Redstart *Phoenicurus ochruros*. *Ardea*. 85:212–221.
- Darwin C. 1871. *The descent of man and selection in relation to sex*. London: Murray.
- Delhey K, Peters A, Johnsen A, Kempenaers B. 2006. Seasonal changes in blue tit crown color: do they signal individual quality? *Behav Ecol*. 17:790–798.
- Dickinson JL, McGowan A. 2005. Winter resource wealth drives delayed dispersal and family-group living in western bluebirds. *Proc R Soc Lond B Biol Sci*. 272:2423–2428.
- Double MC, Cockburn A. 2003. Subordinate superb fairy-wrens (*Malurus cyaneus*) parasitize the reproductive success of attractive dominant males. *Proc R Soc Lond B Biol Sci*. 270:379–384.
- Doucet SM. 2002. Structural plumage coloration, male body size, and condition in the blue-black grassquit. *Condor*. 104:30–38.
- Doucet SM, Montgomerie R. 2003. Multiple sexual ornaments in satin bowerbirds: ultraviolet plumage and bowers signal different aspects of male quality. *Behav Ecol*. 14:503–509.
- Fitzpatrick S. 1998. Colour schemes for birds: structural coloration and signals of quality in feathers. *Ann Zool Fenn*. 35:67–77.
- Griffin AS, Sheldon BC, West SA. 2005. Cooperative breeders adjust offspring sex ratios to produce helpful helpers. *Am Nat*. 166:628–632.
- Hosono T. 1983. A study of the life history of blue magpie. II. Breeding helpers and nest-parasitism by cuckoos. *J Yamashina Inst Ornithol*. 15:63–71.
- Jawor JM, Gray N, Beall SM, Breitwisch R. 2004. Multiple ornaments correlate with aspects of condition and behaviour in female northern cardinals, *Cardinalis cardinalis*, as indicator of condition. *Anim Behav*. 67:875–882.
- Johnsen A, Andersson S, Örnborg J, Lifjeld JT. 1998. Ultraviolet plumage ornamentation affects social mate choice and sperm competition in bluethroats (Aves: *Luscinia s. svecica*): a field experiment. *Proc R Soc Lond B Biol Sci*. 265:1313–1318.
- Keyser AJ, Hill GE. 1999. Condition-dependent variation in the blue-ultraviolet coloration of a structurally based plumage ornament. *Proc R Soc Lond B Biol Sci*. 266:771–777.
- Keyser AJ, Hill GE. 2000. Structurally based plumage coloration is an honest signal of quality in male blue grosbeak. *Behav Ecol*. 11:202–209.
- Kodric-Brown A, Brown JH. 1984. Truth in advertising: the kinds of traits favored by sexual selection. *Am Nat*. 124:309–323.

- Komeda S, Yamagishi S, Fujioda M. 1987. Cooperative breeding in azure-winged magpies, *Cyanopica cyana*, living in region of heavy snowfall. *Condor*. 89:835–841.
- Kose M, Møller AP. 1999. Sexual selection, feather breakage and parasites: the importance of white spots in the tail of the barnswallow (*Hirundo rustica*). *Behav Ecol Sociobiol*. 45:430–436.
- McGraw KJ, Mackillop EA, Dale J, Hauber ME. 2002. Different colors reveal different information: how nutritional stress affects the expression of melanin- and structurally based ornamental plumage. *J Exp Biol*. 205:3747–3755.
- Örnborg J, Andersson S, Griffith SC, Sheldon BC. 2002. Seasonal changes in a ultraviolet structural colour signal in blue tits, *Parus caeruleus*. *Biol J Linn Soc*. 76:237–245.
- Redpath S. 1988. Vigilance levels in preening dunlin *Calidris alpina*. *Ibis*. 130:555–557.
- Rubenstein DR. 2007a. Female extrapair mate choice in a cooperative breeder: trading sex for help and increasing offspring heterozygosity. *Proc R Soc Lond B Biol Sci*. 274:1895–1903.
- Rubenstein DR. 2007b. Stress hormones and sociality: integrating social and environmental stressors. *Proc R Soc Lond B Biol Sci*. 274:967–975.
- Sacarrao GF. 1967. Remarques sur la variation géographique de la Piebleue, *Cyanopica cyanus* (Pall.) dans la Péninsule Iberique, specialment a Portugal. *Arq Mus Bocage*. 1:241–248.
- Shawkey MD, Pillai SR, Hill GE, Siefferman LM, Roberts SR. 2007. Bacteria as an agent for change in structural plumage color: correlational and experimental evidence. *Am Nat*. 169:S112–S121.
- Siefferman L, Hill GE. 2003. Structural and melanin coloration indicate parental effort and reproductive success in male eastern bluebirds. *Behav Ecol*. 14:855–861.
- Siefferman L, Hill GE. 2005a. UV-blue structural coloration and competition for nestboxes in male eastern bluebirds. *Anim Behav*. 69:67–72.
- Siefferman L, Hill GE. 2005b. Blue structural coloration of male eastern bluebirds *Sialia sialis* predict incubation provisioning to females. *J Avian Biol*. 36:488–493.
- Tubaro PL, Lijtmaer DA, Loughheed SC. 2005. Cryptic dichromatism and seasonal color variation in the diademed tanager. *Condor*. 107:648–656.
- Valencia J, Cruz C, Carranza J, Mateos C. 2006. Parents increase their parental effort when aided by helpers in a cooperatively breeding bird. *Anim Behav*. 71:1021–1028.
- Valencia J, Cruz C, González B. 2003. Flexible helping behaviour in the Azure-winged magpie. *Ethology*. 119:545–558.
- Woodcock EA, Rathburn MK, Ratcliffe LM. 2005. Achromatic plumage reflectance, social dominance and female mate preference in black-capped chickadees (*Poecile atricapillus*). *Ethology*. 111:891–900.
- Young AJ, Spong G, Clutton-Brock T. 2007. Subordinate male meerkats prospect for extra-group paternity: alternative reproductive tactics in cooperative mammals. *Proc R Soc Lond B Biol Sci*. 274:1603–1609.
- Zahavi A. 1975. Mate selection—a selection for a handicap. *J Theor Biol*. 53:205–214.
- Zampiga E, Hoi H, Pilastro A. 2004. Preening, plumage reflectance and female choice in budgerigars. *Ethol Ecol Evol*. 16:339–349.