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Original article

Age and breeding success related to nest position in a White stork *Ciconia ciconia* colony

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ABSTRACT

Coloniality is a breeding system that may produce benefits in terms of breeding success, although these advantages could vary according to factors such as colony size or nest position. We studied breeder's age in relation to nest position (peripheral or central) within the colony. In addition, we studied the relationship between breeding success and nest position, controlling for breeder's age, a highly correlated factor, in a White Stork *Ciconia ciconia* colony over a 7-year period. Our results show that central nests are mainly occupied by adult birds and had lower failure rates. However, controlling for breeder's age, nest position per se did not explain breeding success. The scarce predation and the lack of human disturbance in the study colony could explain the absence of differences in breeding success between different nest positions within the colony.

1. Introduction

Many hypotheses have been proposed to explain the evolution and maintenance of coloniality in birds: an increase in mating opportunities (Alexander, 1974; Draulans, 1987), greater familiarity with the quality of breeding sites (Forbes and Kaiser, 1994; Boulinier and Danchin, 1997), or the possibility of extra-pair copulations by females (Wagner, 1992; Hoi and Hoi-Letner, 1997). In addition, colonial breeding should decrease predation (Tenaza, 1971; Burger, 1981; Oro, 1996; Brunton, 1999; Picman et al., 2002; Serrano et al., 2005), increase foraging efficiency (Krebs, 1978), and help to communicate information about the location of food patches (Wittenberger and Hunt, 1985). On the other hand, several costs are associated with coloniality, such as an increased competition for mates, food, or nest material, a higher risk of cuckoldry and intra-specific parasitism, a higher probability of parasite transmission, and increased detection by predators (Alexander, 1974; Burger, 1981; Carrascal et al., 1995; Møller and Birkhead, 1993; Brown and Brown, 1996; Mougeot, 2004).

In most colonial bird species, breeding success is associated with colony size. Larger sub-colonies have a higher breeding outcome than smaller ones (Tenaza, 1971; Young, 1994; Barbosa et al., 1997; Brunton, 1999). However, this pattern is not absolutely general (Hunter, 1991; Emslie et al., 1995; Weaver and Brown, 2005), and physical characteristics of sub-colonies, such as the degree of isolation and slope, as opposed to just size, may also affect breeding success (De Neve et al., in press).

In addition, breeding success is also related to nest position in the colony with individuals in central nests having a higher breeding success than birds in peripheral nests (Tenaza, 1971; Emslie et al., 1995). This has principally been explained by a higher predation rate in peripheral nests (Picman et al., 2002). In accordance with these differences in the reproductive value of nest positions, nest defence has also been found to be higher in central nests than peripheral ones (Viñuela et al., 1995). However, nest position per se, is

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not the only reason for the different breeding success between central and peripheral nests, and other factors such as breeder's age, may also affect this relationship (Ainley et al., 1983; Young, 1994). This interaction is probable as adults are usually better breeders than young birds (Rockwell et al., 1993; Green, 2001; Newton and Rothery, 2002; Reid et al., 2003), and tend to occupy central nests (Spurr, 1975; Ainley et al., 1983; Robertson, 1986; Gibbs et al., 2000). However, studies that analyse the relationship between breeder's age, nest position and breeding success concurrently are very scarce (Ainley et al., 1983; Young, 1994).

In this study, we tested nest position in relation to breeder's age in a White stork *Ciconia ciconia* colony, over a 7-year period. This species can live both in solitary and colonially, although colonialism is more characteristic to southern populations. Based on findings in other bird species, we predict that peripheral nests would principally be occupied by young birds (Spurr, 1975; Ainley et al., 1983; Robertson, 1986; Gibbs et al., 2000). In a previous study of White storks, Vergara et al. (in press), also showed that age was strongly correlated with breeding success in that adults were more successful breeders than young birds. In the current study, we also tested the effect of nest position on breeding success, controlling for the effect of breeder's age, in order to elucidate the effect of both variables.

2. Methods

2.1. Study area and general procedures

The study was carried out in a White stork colony located in the Northern area of the Madrid region, central Spain (40°44′ N, 3°49′ E). The colony is located on private property (cattle farm), and is comprised of an Ashes *Fraxinus* sp. "Dehesa", a traditional Spanish land-use system in which wood collection, livestock raising, and crop production are carried out in the same area (Pardo and Gil, 2005). The study population has increased considerably over the last 16 years, from 2–3 nests in 1989 to 171 in 2005 (Vergara et al., submitted for publication). In the entire Madrid region, the number of White storks increased from 215 breeding pairs in 1984, (Lázaro et al., 1986) to 979–1013 pairs in 2001 (Aguirre and Atienza, 2002) and 1220 pairs in 2004 (Molina and Del Moral, 2005). From 1980 to 2004, 3844 nestlings were ringed in their nests with numbered metal and PVC rings, at an age of 40–50 days. Of these, 349 chicks were ringed with small standard, numbered metal rings with codes that were difficult to read. One hundred forty-four were ringed with large metal rings and 3351 with PVC rings, each with an alphanumeric code legible from a distance of up to 400 m with the use of telescopes. From 1999 to 2005, we watched for ringed, breeding birds within the colony under study and identified them by reading their ring codes with telescopes when perched on their nests during the period from February to July each year. A total number of 217 breeding attempts involving 99 different ringed and sexed individuals were recorded.

Nest position was defined as "peripheral nest (1)" when there were less than two nests between that nest and the border of the colony, and all the other nests were considered as "central nest (0)". *Breeding outcome* was considered as a binary variable with failed nests designated as "0", and successful nests where at least one chick fledged as"1". *Productivity* was defined as the number of nestlings in the nest 40 days after hatching in successful nests (range = 1–5). Over the 7-year period, we monitored 972 breeding attempts (531 from central nests and 441 from peripheral nests) in 219 different nests. The sex of ringed, breeding individuals was determined by observation of copulation behaviour at egg laying (Cramp and Simmons, 1977; Schulz, 1998). Nestlings were sexed by molecular techniques (Fridolfsson and Ellegren, 1999) using DNA extracted from blood obtained by brachial venipuncture during ringing at the age of 40 days. Molecular sexing of nestlings also allowed us to determine the sex of those individuals recorded as breeders in subsequent years. Age was determined by identification of ring codes of individuals marked as nestlings. In order to balance the data, we regarded the last age class as 7 years or older. We obtained six age-classes (2–7).

2.2. Statistical analyses

To determine if breeder's age predicted nest position, we formulated a generalized linear mixed model GLIMMIX with a binomial error distribution (Littell et al., 1996) using SAS statistical software (SAS 1989–96 Institute Inc., Cary, NC, USA). Nest position (peripheral-central) was the response variable, and we included breeder's age (covariate), sex (fixed factor), and their interaction as explanatory variables.

In order to test differences in breeding outcome between nest positions, we again formulated a generalized linear mixed model GLIMMIX with a binomial error distribution. In this model, breeding outcome (failed-successful) was the response variable and nest position was the fixed factor. Nest number was included as a random factor. We repeated this model, including breeder's age (covariate), sex (fixed factor) and the interactions sex*nest position and sex* breeder's age.

A general linear mixed model GLMM was constructed, including productivity (response variable) and nest position (fixed factor). Nest number was included as a random factor. We repeated this model including breeder's age (covariate), sex (fixed factor) and sex*nest position and sex* breeder's age interactions. Productivity does not differ significantly from normal distribution (K-S, $P < 0.05$), but because residuals from the models showed a normal distribution (K-S, $P > 0.05$), the use of GLMMs was suitable.

We conducted analyses at the population level. They included all data across individual birds within years independently of the number of years that particular individuals were recorded as breeders. We considered individual identity as a random factor to avoid pseudoreplication (Hurlbert, 1984). As breeding performance is expected to vary between years, we also considered breeding year as a random factor. As some of the explanatory variables could covary, we fitted their effects to the observed data following backward and forward stepwise procedures, testing the significance of each variable one by one, and removing or adding, respectively, the variables that resulted in the largest increase of model fit. The result is the minimum adequate model

(MAM) for explaining the variance of the response variable, where only significant explanatory variables and two-term interactions were retained. We used the Akaike's Information Criterion (*AIC*; Akaike, 1973) to determine the model that better fit the data, when two alternative models resulted. All tests are two-tailed. Mean values ± S.E are given.

3. Results

Breeder's age explained significant variation in nest position (GLIMMIX $F_{1,112} = 7.52$, $P = 0.0071$, estimate = –0.6689, scaled deviance = 186.57, $AIC = 1328$, $n = 217$). Central nests were more often occupied by adults (Table 1). Sex and the interaction between sex and age were not significantly correlated with nest position ($P > 0.3$, $AIC > 1330$).

Furthermore, nest position explained significant variation in breeding outcome (GLIMMIX $F_{1,763} = 13.65$, $P = 0.0002$, scaled deviance = 1016.95, $n = 972$). Central nests failed less often in breeding than peripheral nests (18.5% ($n = 531$) and 32.2% ($n = 441$) of failed nests, respectively). However, when we included breeder's age in the same model, nest position was no longer significant and only breeder's age significantly explained breeding outcome (Table 2). Sex and all the interactions were not significantly correlated with breeding outcome (Table 2). Due to the fact that age predicted nest position, we analysed the variation in breeding outcome in relation to nest position within each age-class in order to elucidate the effects of both variables. However, nest position did not have a significant effect on breeding outcome in any of the age-classes (all $P > 0.05$).

Productivity did not differ between individuals breeding in central nests and individuals breeding in peripheral nests (2.73 ± 0.04 and 2.63 ± 0.05 nestlings, respectively; GLMM $F_{1,545} = 1.55$, $P = 0.21$, $n = 732$). When we included breeder's age in the same model, nest position was not significant and only breeder's age significantly explained productivity (Table 2). Sex and all the interactions were not significantly correlated with productivity (Table 2).

Table 1 – Average of individuals breeding in peripheral nests, average of successful nests and productivity (mean ± S.E.) in each age-class. Seven years or older individuals are included in the same age-class. Sample sizes (number of individuals) are given in parentheses

Age class	% Peripheral nests	% Successful nests	Productivity
2	47.05 (34)	41.76 (34)	2.21 ± 0.15 (14)
3	58.33 (60)	61.66 (60)	2.08 ± 0.13 (37)
4	42 (50)	90 (50)	2.66 ± 0.14 (45)
5	40 (25)	92 (25)	2.65 ± 0.26 (23)
6	20 (15)	86.66 (15)	2.84 ± 0.19 (13)
7+	36.36 (33)	84.84 (33)	3.17 ± 0.13 (28)

4. Discussion

4.1. *Nest position and age*

Our results show that peripheral nests are primarily occupied by young White storks, which is in accordance with findings in other colonial bird species (Spurr, 1975; Ainley et al., 1983; Robertson, 1986; Gibbs et al., 2000). Previous studies suggested that this age difference in nest position probably arises from the fact that young birds generally arrive later to the colony (Ainley et al., 1983; Robertson, 1986; Minguez et al., 2001). In addition, and also in accordance with previous findings in other colonial bird species, breeding outcome was higher in central nests than in peripheral nests (Tenaza, 1971; Aebischer and Coulson, 1990; Emslie et al., 1995). However, our results indicate that breeder's age, being related to nest position, may have played a role in these differences. When both age and nest position were included in the analyses, only age explained significant variation in breeding outcome. Thus, nest position did not explain breeding outcome when analysed in the separate age-classes, suggesting that it was age rather than nest position per se that affected breeding outcome. In fact, older White storks in Spanish populations generally show higher breeding success than young birds (Vergara et al., in press). In addition, our results show that older breeders with higher breeding success occupy better quality nests in accordance with previous studies (Tryjanowski et al., 2005). Other nest characteristics should be addressed in future studies to establish why some nests are occupied more often than others.

Additionally, although breeding success was lower in peripheral nests, unexpectedly, productivity did not differ between nests. A possible explanation could be a senescence effect, i.e. older individuals usually produce a lower number of fledglings but show a higher breeding success (Forslund and Pärt, 1995). Hence, older birds breeding in central nests have lower productivities, which are similar to those of young storks breeding in peripheral nests. Lower productiv-

Table 2 – Results of the mixed models in which breeding outcome and productivity were the response variables. § Final model. Breeding outcome: GLIMMIX, scaled deviance = 198.20, *AIC*: Final model = 1053, Candidate models > 1055; *n* = 217. Productivity: GLMM, *AIC*: Final model = 429, Candidate models > 431; *n* = 160

Response variable	Explanatory variables	Df	F	Estimate	P
Breeding outcome	*Breeder's age§*	1,109	15.93	0.5421	**0.0001**
	Nest position	1,109	0.03	0.4740	0.8547
	Sex	1,109	0.20	–0.0586	0.6560
	Sex*nest position	1,109	0.55	–0.8450	0.6500
	Sex* breeder's age	1,109	0.30	0.1856	0.5825
Productivity	*Breeder's age§*	1,70	22.12	0.2184	**< 0.0001**
	Nest position	1,70	0.45	–0.0861	0.5065
	Sex	1,70	1.21	–0.3684	0.2759
	Sex*nest position	1,70	0.26	–0.0358	0.9079
	Sex* breeder's age	1,70	0.24	0.0503	0.6239

ity in older birds might decrease the mean values of productivity in central nests. However, we did not find the expected decrease in productivity (Table 1), probably because we did not record older individuals (10 or more years), which in the White stork, are the age-classes in which productivity decreases (Aguirre and Blanco, in preparation). Chick ringing in the colony started in 1999. For that reason, ringed individuals older than 6 years, are scarce. In conclusion, our results support the idea that breeder's age may be a relevant factor explaining breeding success differences between nest positions in the colony (Ainley et al., 1983; Young, 1994).

4.2. *Are peripheral nests a disadvantage?*

In other species, it has been repeatedly suggested that predation is one of the main causes of lower breeding success in peripheral nests (Picman et al., 2002). This is because peripheral nests are more accessible to predators (Picman et al., 2002). However, in our study colony, predation is very scarce, occurring in less than 5% of nests (personal observation), and hence, predation probably does not affect breeding success in any significant way. Another potential factor that could affect breeding in relation to nest position is human disturbance. However, our study colony is on a private property with very little human disturbance (personal observation). Thus, it is unlikely that there would be varying levels of disturbance between central or peripheral nests. Therefore, both of these environmental factors (scarce predation and absence of human disturbance) could help to explain why nest position per se did not have an effect on breeding success in our study population. Blackmer, 2004; Saetre, 1996; Tryjanowski, 2004.

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