



Arrival date, age and breeding success in white stork *Ciconia ciconia*

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Early arrival to breeding grounds is a life history trait in birds that can result in fitness benefits. We studied the relationship between arrival date and breeding success of individuals in a central Iberian population of white stork *Ciconia ciconia*, between 1999 and 2005, and the ways in which other potential factors, such as age or sex, affect this relationship. Our results showed that age was the factor most closely related to arrival date and breeding success. Older individuals returned earlier to the breeding grounds, achieved larger clutch sizes and produced more chicks than younger birds. After controlling statistically for age effect, breeding probability (laid eggs or not) and laying date were still significantly explained by arrival date. A higher probability of failure to reproduce (no eggs laid) was found in birds arriving later than in those arriving early. However, clutch size and nestling success (number of nestlings in the nest 40 days after hatching) were not correlated with arrival date. Food availability in the study area throughout the breeding cycle, due to a nearby rubbish dump, could be the factor mitigating differences in clutch size and nestling success related to individual arrival date.

Arrival date in migratory birds is a life-history trait that affects individuals' fitness through reproductive success. In addition, early arrival to the breeding areas in long-distance migratory birds is usually associated with higher breeding success (Hotker 2002). One possible explanation is that individuals arriving earlier to the breeding grounds are in better condition (Ninni et al. 2004) or have lower parasite infestation (Møller et al. 2004) than later individuals. However, reproductive benefits of an early arrival could be offset by some potential factors that might affect breeding areas, such as nest predation and parasitism rates (Palomino et al. 1998) or such as rough weather conditions that increase adult mortality rates and maintenance costs (Møller 1994, Brown and Brown 2000), or that decrease food availability (Béty et al. 2004).

Therefore, food availability is likely one of the main factors influencing arrival date in birds, which in turn could depend on the environmental conditions encountered by individuals in their wintering quarters, stopover sites and breeding areas (Ahola et al. 2004, Hubalek 2004, Saino et al. 2004, Both et al. 2005, Gordo et al. 2005, Zalakevicius et al. 2006). A seasonal

decrease in clutch size was reported for several bird species caused by reduced food availability during the breeding season (Korpimäki and Wiehn 1998, Siikamäki 1998). However, in some western populations of white stork *Ciconia ciconia* this hypothesis was not confirmed and laying date had little effect on clutch size (Tortosa et al. 2003, Massemin-Challet et al. 2006). In these populations, food resources are accessible throughout the breeding cycle due to rubbish dumps upon which storks feed (Blanco 1996, Tortosa et al. 2002, 2003, Peris 2003) or supplementary food provided by humans (Massemin-Challet et al. 2006). If food availability is no longer a handicap for this species, and if migration is an adaptive strategy to adequately satisfy the food demands of individuals with temporal food resources (Pérez-Tris and Telleria 2002), it is possible that their migratory strategies might differ accordingly. A change of migratory strategy is occurring in the Iberian population of white stork. A growing number of individuals have overwintered in Spain since the mid-1980s (Martínez 1994, Tortosa et al. 1995, Prieto 2002, Vergara et al. 2004), which has probably advanced arrival dates as a whole (Gordo and Sanz

2006). However, the relationship between arrival date and breeding success has not yet been studied.

The aim of this study is to analyse the effect of arrival date on breeding success in one segment of the Iberian population of white stork with access to food resources throughout the breeding season due to the presence in their breeding area of a rubbish dump on which they feed. We examined the relationship of breeding probability (laid eggs or not), laying date, clutch size or number of nestlings in the nest 40 days after hatching to the date of arrival to the breeding grounds, and whether or not there are sexual and age-class differences in such traits. If food resources are accessible to all individuals independent of their age or social status (Prieto 2002), and if these resources are constant throughout the season (Martínez 1994, Prieto 2002), we predict that arrival date will have little effect on breeding success in this species. Nevertheless, we controlled for breeder's age as this is a factor related to both arrival date and breeding success in this species (Bernis 1959, Barbraud and Barbraud 1999, Vergara et al. 2006).

Methods

Study area and general procedures

The study was carried out in the province of Madrid (7740 km²) in Central Spain. In this area, the number of white storks increased from 215 breeding pairs in 1984, (Lázaro et al. 1986) to 1220 pairs in 2004 (Molina and del Moral 2005). White stork breeding pairs have been monitored in our study area since 1989. Chick ringing with metal and PVC rings has been carried out since 1980. The area under study is five kilometres away from the second largest rubbish dump in the province of Madrid (Colmenar Viejo, 40. 39N 3. 44W). Nests (solitary or colonial) and the rubbish dump in the study area were checked every 7–15 days between December and June from 1999 to 2005 in order to record arrival date to the breeding grounds of ringed individuals. Arrival date was defined as the day of the first observation of an individual by identifying its PVC ring, designating the first of December as value "1". When a bird had been observed in one visit, its detection probability in the following visit was 56.1%, with no differences between younger (1–6 years old) or older (7+) birds ($\chi^2=0.03$, $P=0.8$). In addition, average detection probably in breeders (see later) was $71.73\% \pm 22.54$ (mean ± 1 SD). Detection probability = $100 \times$ number of visits to the colony in which one individual is detected since their arrival date/total number of visits to the colony since arrival day of the individual (see Bêty et al. 2003 for a similar approach). The sex of ringed breeding individuals was

determined by the observation of copulatory 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 banding at the age of 40 days. Molecular sexing of nestlings also allowed us to identify their sex when recorded as breeders in subsequent years. Age was determined by identification of ring codes of individuals marked as nestlings. Marked individuals ranged from 1 to 19 years old.

Breeding variables

We considered as breeders those individuals that were observed constructing, defending or perching on nests (but see Wuczyński 2005). We monitored nests with ringed breeders by several visits to record breeding performance. Breeding probability was defined as "1" if eggs were found, or "0" if no eggs were found in nests with a breeding pair. Less than 4% of the nests were predated upon during the study period and early abandonment is rare in our population and study area (authors' unpubl. data). Hence, it is most likely that if no eggs were found, then individuals, in fact, did not lay eggs. Laying date was defined as the day on which the first egg was laid. It was recorded or estimated according to a regression equation using peak length (age = $-5.649 + 0.455 \times$ peak length, $R=0.90$, $n=547$, $P<0.001$) and subtracting the average incubation period (mean 32 days, Bernis 1981, Schulz 1998). Clutch size (range = 1–5) was also monitored. Nestling success was defined as the number of nestlings in the nest 40 days after hatching (range = 0–4), including only those nests with egg-laying confirmed. The only one-year old breeder and the only nest with six eggs and five nestlings were excluded from the models. All breeding variables were estimated only in breeders.

Statistical analyses

In order to test differences in arrival date, we formulated a general linear mixed model (GLMM) using SAS statistical software (SAS 1989–96 Institute, USA). We analysed the relationship between arrival date (response variable), sex (fixed factor), age and the squared term of age (covariates). We also applied a general linear mixed model (GLMM) to test the relationship between laying date (response variable) and arrival date (covariate). Age, squared term of age (covariates), and sex (fixed factor) were included in the model. To test the effects of arrival date in breeding probability we applied a generalized linear mixed model (GLIMMIX) with binomial error distribution (Littell et al. 1996). Breeding probability (response variable),

sex (fixed factor), age, squared term of age and arrival date (covariates) were included in the model. Finally, we used GLMMs to analyse the effect of arrival date on clutch size and nestling success. Two models were constructed including clutch size and nestling success (response variables), arrival date, laying date, age, squared term of age (covariates), and sex (fixed factor). We included the squared term of age because a quadratic pattern has been observed in numerous bird species between breeding performance and age (Forslund and Pärt 1995) and also in the Iberian populations of White stork (Aguirre 2006). In all models where significant quadratic effects were found, the quadratic function resulted in larger R^2 values for the models than other linear or curvilinear functions. Only in the model including arrival date as the response variable did hyperbolic function explain higher variance than quadratic function (or other functions, see results). When variables did not present a normal distribution (Lillefors $P < 0.05$), we checked residuals from the models. In all cases, residuals showed a normal distribution (Lillefors $P > 0.05$), for which the use of GLMMs was suitable. To test if sex affects the variables under study, we also included the interaction between sex and the variables included in each model.

In many cases the same individual was recorded in two or more years, hence we included individual as a random factor in all models to avoid pseudo-replication (Hurlbert 1984). We recorded 22 cases with marked males and marked females breeding together. In these cases, we only included one individual randomly selected from each pair in the analysis, except in the model in which arrival date was the response variable, where all cases were included. As breeding performance and arrival date 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 minimal adequate model (MAM) for explaining the variance of the response variable, where only significant explanatory variables and two-term interactions were retained. By performing forward and backward procedures we can explore the possible error of the variance inflation due to the collinearity of variables (Quinn and Keough 2002). All the analyses were two-tailed. Means \pm SE are given.

Results

We achieved 654 observations of arrival dates, corresponding to 228 different individuals (123 males and

105 females). Another 333 observations of 224 individuals of unknown sex were recorded. Also, 139 ringed individuals were recorded as breeders (74 males, 52 females and 13 individuals of unknown sex) in 285 breeding attempts. We were able to record arrival date and laying date in 88 breeding attempts from 50 ringed individuals (including individuals of unknown sex). Clutch size and nestling success were reported in 81 and 87 breeding attempts in 48 and 50 individuals, respectively (only including ringed individuals of known arrival and laying date; individuals of unknown sex were included).

The relationship between arrival date and age (including individuals of unknown sex) was better explained by a hyperbolic function ($R^2 = 0.59$, Fig. 1) than by a quadratic ($R^2 = 0.57$), asymptotic ($R^2 = 0.36$), exponential ($R^2 = 0.57$) or linear ($R^2 = 0.39$) function. Arrival date showed a steep decline from age "1" to age "6–8", followed by a plateau (Fig. 1). Hence, we did not include the squared term of age in the model and we performed different models to determine the age-class in which arrival date is not statistically related to age. With this purpose we constructed models including all age-classes, excluding age-class 1, excluding age-class 1 and 2, and so on. The first model in which arrival date was not statistically related to age ($P > 0.1$), was the model including age-class 6 or more (Table 1). Arrival date was strongly correlated with age before age-class 6 (Table 1), with older storks arriving earlier than younger ones, but not after (all $P > 0.1$, Fig. 1). Beginning from age class 6, sex explains differences in arrival date, females arriving earlier than males, although not significantly so (all P between 0.06 and 0.1).

Laying date was significantly explained by arrival date, age and the squared term of age with older and early arrivers laying earlier than younger and later ones (Table 2). Sex and all the studied interactions were not correlated with laying date (all $P > 0.2$). Breeding probability was significantly explained by arrival date, age and the squared term of age (Table 2). Controlling for breeder's age, individuals that laid eggs, arrived earlier than individuals that did not lay them. Sex and all the studied interactions were not correlated with breeding probability (all $P > 0.4$). In order to elucidate the effect of age and arrival date, both variables were analysed exploring the variation in breeding probability within each age-class. Arrival date had a significant effect only in age group two (GLIMMIX, $F_{1,26} = 6.39$, $P = 0.02$, estimate = -0.05 , $n = 32$, 113.7 ± 7.8 and 84.8 ± 4.9 mean arrival date for individuals with no eggs found and eggs found, respectively), but not in the remaining age-classes (all $P > 0.1$).

Finally, laying date tended to explain differences in clutch size that decreased as laying date was later, but nestling success was not significantly explained by

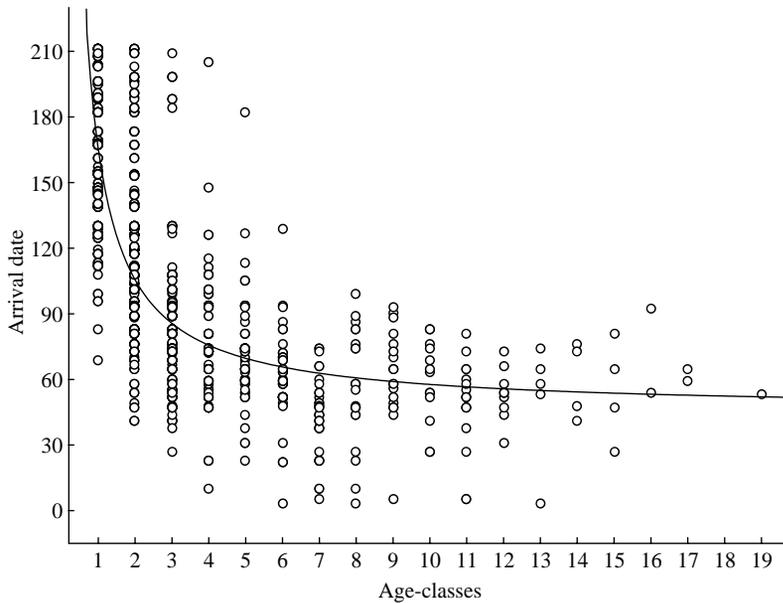


Fig. 1. Correlation between arrival and the age of breeders in years adjusted according to the hyperbolic function; $y = (45.75) + ((119.49)/x)$. Arrival date 1 = 1st of December.

arrival date (Table 3), controlling for age and the squared term of age. Older individuals laid larger clutches and produced more chicks than younger individuals. Sex and the studied interactions were not significantly correlated with clutch size or nestling success (all $P > 0.1$).

Discussion

We found evidence that the breeding probability and laying date were correlated with arrival date, controlling for the effect of breeder's age. Our results are in agreement with previous studies in other migratory bird species in which individuals arriving earlier to the breeding grounds have the highest reproductive success (Potti 1998, Forstmeier 2002, Hotker 2002, Bêty et al. 2004). Individuals in better condition are usually the first ones to arrive at the breeding grounds (Møller

2001, Møller et al. 2004). By increasing the time available to accumulate resources, they develop a better physical condition before breeding. Hence, early arriving individuals should achieve higher breeding success than later ones due to the fact that they acquire high quality territories and consequently high quality females (Aebischer et al. 1996), likely due in part to their better body condition (Bêty et al. 2004). Nevertheless, more research controlling for breeder's body condition is necessary to establish more thorough conclusions.

However, arrival date has no effect on the rest of the studied breeding performance parameters (clutch size and nestling success), contrary to previous studies in this species in Poland which concluded that breeding success (measured as the number of fledglings produced) were correlated to arrival date (Kosicki et al. 2004, Trijanowski et al. 2004). Our limited accuracy in the arrival estimates may partly explain why we found no relationships between arrival date and the number of

Table 1. Results of the general liner mixed models (GLMM) in which arrival date was the response variable. Values from non-significant variables corresponding with the point at which they were removed from model. More details in text.

Age-classes	Explanatory variables			
	Age	Age × sex	Sex	n
All	$F_{1,417} = 326.94$, $P < 0.001$, estimate = -24.21	$F_{1,417} = 9.21$, $P = 0.002$	$F_{1,417} = 0.54$, $P = 0.5$	654
2+	$F_{1,324} = 91.38$, $P < 0.001$, estimate = -4.60	$F_{1,323} = 2.45$, $P = 0.1$	$F_{1,324} = 0.38$, $P = 0.5$	544
3+	$F_{1,211} = 34.09$, $P < 0.001$, estimate = -2.44	$F_{1,210} = 0.40$, $P = 0.5$	$F_{1,211} = 1.05$, $P = 0.3$	403
4+	$F_{1,126} = 12.74$, $P < 0.001$, estimate = -1.59	$F_{1,125} = 0.29$, $P = 0.6$	$F_{1,126} = 1.45$, $P = 0.2$	264
5+	$F_{1,85} = 2.63$, $P = 0.1$, estimate = -0.84	$F_{1,84} = 0.84$, $P = 0.4$	$F_{1,84} = 0.48$, $P = 0.5$	167
6+	$F_{1,63} = 0.11$, $P = 0.7$, estimate = 0.23	$F_{1,62} = 0.02$, $P = 0.9$	$F_{1,64} = 2.14$, $P = 0.1$	120

Table 2. Results of the mixed models in which laying date (GLMM, n = 88) and breeding probability (GLIMMIX, n = 285) were the response variables. Only significance variables are presented (more details in text).

Explanatory variables	Response variable							
	Laying date			Breeding probability				
	df	F	P	Estimate	df	F	P	Estimate
Arrival date	1,24	7.12	0.01	0.11	1,121	10.82	0.001	-0.04
Age	1,24	17.59	<0.001	-6.18	1,121	10.30	0.002	1.85
Age ²	1,24	10.96	0.003	0.36	1,121	7.95	0.006	-0.12

fledglings produced, contrary to the previous mentioned studies. On the other hand, food availability, due to the presence of a rubbish dump in our study area, may be the reason for such variation between study areas. One of the factors that might counteract the benefits of early arrival is low food availability (Bêty et al. 2004). Seasonal decrease in clutch size was observed in several bird species (Korpimäki and Wiehn 1998, Siikamäki 1998). Clutch size only increased in situations with additional food supply when natural resources were scarce (Hiom et al. 1991, Svensson and Nilsson 1995, Nager et al. 1997). We found that clutch size decreased as laying date increased, however not significantly, as in other populations of Iberian storks (Tortosa et al. 2003). Recently, Massemin-Challet et al. (2006) have found a similar effect in the Alsace region of northeastern France. Here, white storks did not present a relationship between laying date and clutch size when they fed on rubbish dumps or when they had access to supplementary food supplies from humans. The minimal effect of laying date in clutch size is likely due to the lack of seasonal variation in food resources on account of the presence of rubbish dumps (Martínez 1994, Tortosa et al. 1995, 2003). Later arriving individuals with presumably inferior body condition than earlier arriving individuals may compensate their late arrival by feeding on the rubbish dumps and consequently, laid similar clutch sizes to earlier birds. Also, food accessibility throughout the annual cycle means that individual birds will be able to feed their chicks successfully, independent of their arrival date. The absence of strong competition among breeders for

this resource could assist in the understanding of our hypothesis. However, these particular aspects require further research.

In addition, age is strongly correlated with arrival date in the White stork (see Fig. 1; Bernis 1959, Barbraud and Barbraud 1999), although our results showed that at older age-classes (age-class 6 or higher), arrival date is not statistically related to age. Sexual maturity of this species occurs at 2–5 years old in our population (Prieto 2002). Hence, it is likely that non-breeders, arrive later than breeders to avoid the potential costs of an early arrival such as an increase in mortality rates and maintenance costs (Møller 1994, Brown and Brown 2000). Additionally, older individuals are more successful breeders than younger ones (Vergara et al. 2006; this study). Therefore, it is essential to account for breeder's age in the study of the relationship between arrival date and breeding success in this species, at least in the Iberian populations, in order to avoid bias caused by differential behavior between age-classes.

Finally, we found no sex differences in arrival date in young age-classes, contrary to previous studies in this species (Barbraud and Barbraud 1999, Barbraud et al. 1999). The difference in the mean arrival date between sexes in those studies was less than seven days (Barbraud and Barbraud 1999). The reason for the absence of sex differences in young age-classes in our study could be due to the low frequency of visits to rubbish dumps (7–15 days). However, we found that in older age-classes females arrived earlier than males, although not significantly so. Even though it has been confirmed that

Table 3. Results of the general liner mixed models (GLMM) in which clutch size (n = 81) and nestling success (n = 87) were the response variables. Only arrival date, laying date and significance variables are presented (more details in text). § Final model. Values from non-significant variables corresponding with the point at which they were removed from model.

Explanatory variables	Response variable							
	Clutch size			Nestling success				
	df	F	P	Estimate	df	F	P	Estimate
Arrival date	1,18	0.01	0.9	0.01	1,23	0.93	0.3	-0.01
Age	1,19	9.39	0.008§	0.56	1,24	12.80	0.001§	0.65
Age ²	1,19	8.43	0.01§	-0.04	1,24	9.00	0.006§	-0.04
Laying date	1,19	2.88	0.1§	-0.02	1,22	0.59	0.4	0.01

the White stork is changing its migratory patterns (Marchamalo 1994, Tortosa et al. 1995, Sánchez et al. 1994, Vergara et al. 2004, Gordo and Sanz 2006), no sexual segregation of migration has been studied for this species. This must be addressed in future studies, as our data set, principally for old age-classes, is not large enough to draw strong conclusions in this regard.

Acknowledgements – Owners and workers of Prado Herrero farm (Soto del Real, Madrid) where most of our data was collected. Eva Banda and students of the Faculty of Biology of the Universidad Complutense de Madrid helped during the fieldwork. Sexing was partially financed by Guillermo Blanco from the Instituto de Investigación en Recursos Cinegéticos (CSIC). Sarah Young reviewed the English. J.A. Fargallo, L. de Neve and O. Gordo suggested interesting ideas. Joël Bêty and three anonymous referees substantially improved the manuscript.

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