Ibis (2006), **148**, 672–677

Nest-site fidelity and breeding success in White Stork *Ciconia ciconia*

PABLO VERGARA,[1]* JOSÉ I. AGUIRRE,[1] JUAN A. FARGALLO[2] & JOSÉ A. DÁVILA[3]
[1] *Dpto. de Zoología y Antropología Física, Facultad de Biología, Universidad Complutense de Madrid, C/José Antonio Novais, 2, 28040 Madrid, Spain*
[2] *Dpto. de Ecología Evolutiva, Museo Nacional de Ciencias Naturales (CSIC), J. Gutiérrez Abascal 2, E-28006 Madrid, Spain*
[3] *Instituto de Investigación en Recursos Cinegéticos (CSIC), Ronda de Toledo s/n, 13005 Ciudad Real, Spain*

Nest-site fidelity is a life-history trait of birds that may produce benefits in terms of fitness. We studied the relationship between breeding success and nest fidelity in the White Stork *Ciconia ciconia*. We also studied how other factors such as age, sex, habitat, colony size and productivity in previous breeding attempts might interfere with this relationship. Our results showed that pairs with higher fidelity rates also have lower failure rates, and that breeding failure and productivity in the previous season influenced the frequency of nest change in the following season. In addition, a curvilinear relationship was found between age and nest fidelity. These results suggest that age is a major factor related to nest fidelity and therefore individual experience could explain this behaviour in the White Stork. Changing the nest involves a reproductive cost for which nest fidelity can be considered as an adaptive strategy to increase fitness.

Nest-site fidelity is considered to be an adaptive strategy in numerous groups of birds such as Procellariiformes (Bried *et al.* 2003), Anseriformes (Blums *et al.* 2002) and Ciconiiformes (Cezilly *et al.* 2000). One of the functions proposed to explain this behaviour is the strengthening of pair bonds and therefore mate retention (Cezilly *et al.* 2000), which could result in higher survival rates for adults (Ens *et al.* 1993, Bried *et al.* 2003) and/or a contribution to the maintenance of the social status (Heg *et al.* 2003). Furthermore, the maintenance of nest-sites over successive breeding seasons is related to low rates of ectoparasitism (Barclay 1988, Rendel & Verbeek 1996) and/or predation risks, as nest predators have a long-term memory for rewarding nest-sites (Sonerud & Fjeld 1987).

One factor that might affect nest-site fidelity is breeding success in the previous season. Pairs failing to produce, or producing fewer, offspring in a given season tend to be more likely to change nest-sites before the next breeding season (Blums *et al.* 2002, Johannesen *et al.* 2002, Beheler *et al.* 2003, Hoover 2003). Therefore, nest-site fidelity could also be determined by age, as younger individuals tend to have more breeding attempt failures than adults (Rowley 1983, Pyle *et al.* 2001). By contrast, older individuals produce fewer offspring due to the effect of senescence (Forslund & Pärt 1995, Reid *et al.* 2003). Productivity, as a component of breeding success, could also modulate nest-site fidelity behaviour. Similarly, colony size has been proposed as a determinant of breeding performance in birds (Wittenberg & Hunt 1985). Although there are costs associated with the increased size of the colony, such as high rates of parasite transmission, and competition for food or for nest material (Burger 1981, Carrascal *et al.* 1995, Brown & Brown 1996), breeding success is, in general, higher in larger subcolonies, probably because colony size reduces predation risk (Barbosa *et al.* 1997, and references therein). Hence, colony size could mediate nest-site fidelity via breeding success. Other factors such as sex, breeding density, habitat or nest characteristics have also been found to be related to nest-site fidelity (Switzer 1993, Dubois *et al.* 1998, Jouventin & Bried 2001, Pyle *et al.* 2001, Johannesen *et al.* 2002, Beheler *et al.* 2003).

In the White Stork *Ciconia ciconia*, nest-site fidelity has been reported in over 80% of individuals (Barbraud *et al.* 1999). In this species, changes of nest are more frequent in young individuals and are usually followed

*Corresponding author.
Email: mcnpv752@mncn.csic.es

by mate changes, although changes in nest-site have also been observed among different breeding attempts but with no particular reasons identified for that behaviour (Schulz 1998). To date, there have been no studies focused specifically on the factors affecting nest-site fidelity in White Storks. The aim of this study was to explore the applicability, for a long-term monitored population of White Storks, of some of the factors thought to affect nest-site fidelity in birds.

First, we tested whether breeding failure or productivity in the previous breeding season affected nest-site fidelity. If breeding failure does affect nest-site fidelity, we predict higher nest-site fidelity rates in adult than in young individuals. If productivity affects nest-site fidelity, we predict a curvilinear relationship between nest-site fidelity and age. If changes in nest-site are performed to increase breeding success, we also predict higher breeding failure and/or lower productivity in pairs that subsequently change nest than in pairs that do not. In addition, if colony size affects breeding success, nest-site fidelity should be correlated with this variable. Finally, we analysed the relationships between nest-site fidelity and other variables, such as sex and habitat type.

METHODS

The study was carried out in the province of Madrid (7740 km^2), central Spain. In this area the number of White Storks increased from 215 breeding pairs in 1984 (Lázaro *et al.* 1986) to 979–1013 pairs in 2001 (Aguirre & Atienza 2002) and 1220 pairs in 2004 (J.I. Aguirre unpubl. data). White Stork breeding has been monitored in our study area since 1989. Chick ringing with metal and PVC rings has been carried out since 1980. Nests in the study area (solitary or colonial) were checked from 1989 to 2004 in order to record ringed individuals and the number of nestlings produced. For this purpose we used binoculars (8 × 30) and telescopes (20 × 30–60). In total, 170 ringed individuals were identified as breeders.

Nest-site fidelity was defined as the permanence of an individual in the same nest in two consecutive breeding seasons. Breeding outcome was considered as a binary variable, where '0' was assigned to failed nests and '1' to successful nests. Nests in which none of the eggs hatched were considered as failed nests. Productivity was defined as the number of nestlings 40 days after hatching in successful nests (range = 1–4). Only four pairs produced more than four nestlings. These cases were included in the highest productivity category (4). The size of the colony was defined as the number of nests. We considered 'urban' and 'countryside' as two different breeding habitats. The sex of ringed breeding individuals was determined by observation of copulatory behaviour at egg-laying (Cramp & Simmons 1977, Schulz 1998). Nestlings were sexed by molecular techniques (Fridolfsson & 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 know the sex of some breeding individuals in subsequent years. Age was determined by identification of band codes of individuals marked as nestlings.

In order to analyse nest-site fidelity we formulated generalized linear mixed models (GLIMMIX) with binomial error distributions (Littell *et al.* 1996) using SAS statistical software (SAS 1989–96 Institute Inc., Cary, NC, USA), in which nest-site fidelity was included as the response variable. As potential explanatory variables we considered sex, habitat type, breeding outcome of the previous year (fixed factors), and colony size and age (covariates). A second model was similarly performed by using the productivity of the previous year as a covariate, instead of breeding outcome of the previous year.

To improve the function explaining the relationship between age and nest-site fidelity, we estimated the proportion of individuals that did not change nest in each age class. Age classes showed different sample sizes, for which the contribution of each age class to the models was unequal. The analysis was adjusted by weighting the values by the number of individuals in each age class.

In order to determine whether breeding outcome was associated with nest-site fidelity, we constructed generalized linear mixed models (GLIMMIX) with a binomial error distribution with breeding outcome as the response variable. As potential explanatory variables we used nest-site fidelity, sex, habitat type (fixed factors) and colony size (covariate). The bird's age and the squared term of age were included in the model to test for the effect of senescence. We constructed general mixed models (GLMM) with productivity as the response variable. Nest-site fidelity, sex, habitat type (fixed factors) and colony size (covariate) were again included in the model. Age and its squared term were again included in the model. As productivity did not present a normal distribution (K-S, $d = 0.21$, $P < 0.01$), residuals from all GLMM were checked. All the residuals were distributed normally (K-S, all $d < 0.08$, all $P > 0.05$).

In many cases the same individual was recorded in two or more years, for which we included individual (ring number) as a random factor in all models to avoid pseudoreplication. As breeding performance is expected to vary among years, we also considered breeding year as a random factor. As some of the explanatory variables could co-vary, 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 which model best fitted the data. All analyses were two tailed. Two-year-old individuals were excluded from the analyses due to the low sample size ($n = 2$). In order to balance the data we regarded the last age class as 14 years or older.

RESULTS

Nest-site fidelity was observed in 344 cases (79.6%) of 432 records (Table 1). Nest-site fidelity was explained significantly by the breeding outcome of previous years and age (GLIMMIX, Breeding outcome: $F_{1,132} = 18.51$, $P < 0.0001$, *estimate* = –1.5275; age: $F_{1,132} = 14.80$, $P = 0.0002$, *estimate* = 0.2843; model: *scale deviance* = 216.93, $n = 245$). Older individuals producing one nestling at least during the previous year tended to change the nest less often. Sex showed a marginally significant effect on nest fidelity (GLIMMIX, $F_{1,132}$ = 3.02, $P = 0.086$, *estimate* = –0.6127) with females tending to change more than males. Akaike's information criterion showed that the model excluding sex as an explanatory variable fitted the data better (AIC = 1219.4) than the model including it (AIC = 1231.4). The remaining variables were not significantly correlated with nest-site fidelity (all $P > 0.1$). Age and breeding outcome of the previous year were intercorrelated (GLIMMIX, $F_{1,152} = 15.96$, $P = 0.0001$, *estimate* = 0.2874). In order to disentangle the effect of both variables we analysed the variation in nest-site fidelity within each age class. Breeding outcome of the previous year had a significant effect at 4 years of age (GLIMMIX, $F_{1,44} = 8.43$, $P = 0.0057$, *estimate* = –1.8746), 7 years of age (GLIMMIX, $F_{1,16} = 6.06$, $P = 0.02$, *estimate* = –4.0833) and 9 years of age (GLIMMIX, $F_{1,9} = 4.81$, $P = 0.05$, *estimate* = –4.3413), but not in the remaining age classes (all $P > 0.1$).

When we replaced breeding outcome by productivity of the previous year in the model, the latter had a significant effect on nest-site fidelity only through the interaction with sex (GLIMMIX, productivity × sex $F_{2,84} = 3.50$, $P = 0.03$, *estimate* = –0.8452). More productive, and male, individuals tended to change the nest less frequently. Sex showed a marginally significant effect on nest fidelity ($P = 0.16$), females tending to change more than males. According to Akaike's criterion the model including sex fitted the data better (AIC = 1310) than that excluding sex (AIC = 1335.5). Thus, we accepted the model including sex as the final model (GLIMMIX, productivity × sex $F_{2,84} = 3.69$, $P = 0.029$, *estimate* = –0.8452; age $F_{1,84} = 19.75$, $P < 0.0001$, *estimate* = 0.8670; sex $F_{1,84} = 2.01$, $P = 0.16$, *estimate* = 3.0018; model: *scale deviance* = 151.97, $n = 181$).

Age and productivity of the previous year were intercorrelated (GLMM, $F_{1,98} = 6.31$, $P = 0.01$, *estimate* = 0.2915). In order to disentangle the independent effects of these variables we analysed the variation in nest-site fidelity due to productivity of the previous year within each age class (similarly to the analysis with breeding outcome of the previous year). Productivity of the previous year was not significant in any age class (all $P > 0.2$).

The proportion of individuals not changing the nest was positively correlated with age ($F_{1,398} = 235.28$, $P < 0.0001$). This relationship was explained better by a hyperbolic function ($R^2 = 0.81$, Fig. 1) than by a linear ($R^2 = 0.60$) or quadratic ($R^2 = 0.73$) function.

Controlling for age and the squared term of age, breeding outcome was significantly affected by nest-site fidelity (GLIMMIX, $F_{1,144} = 8.55$, $P = 0.004$, *estimate* = 1.067; model: *scale deviance* = 237.9, n = 283). Breeding outcome was significantly lower in individuals that changed their nest-sites (mean ± se, 0.68 ± 0.04) than in those that retained the nest (0.86 ± 0.02). The remaining variables were not significantly correlated with breeding outcome (all $P > 0.5$). Productivity (controlling for age and the squared term of age) was not affected by nest-site

Table 1. Summary of the number of observations. The number of different individuals for each class is given in parentheses.

Sex	No. observed fidelity	No. observed switching	Total
Males	117 (49)	33 (25)	150 (56)
Females	104 (39)	37 (31)	141 (51)
Undetermined	123 (57)	18 (15)	141 (63)
Total	344 (145)	88 (71)	432 (170)

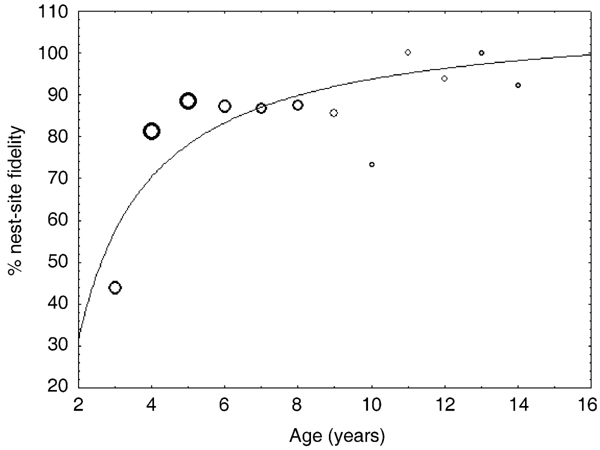

Figure 1. Correlation between age of breeders in years and the percentage of cases with nest-site fidelity, weighted by the number of observations for each age class and adjusted according to the hyperbolic function $y = (109.31) + (-155.74)/x$. Number of cases is represented by different sized symbols (10–15, 16–20, 21–30, 31–40, 41–50 and > 51).

fidelity ($P = 0.3$), but was correlated with the interaction between sex and age (GLMM, $F_{1,155} = 4.02$, $P = 0.046$, *estimate* = 0.038; $n = 271$). Females and older individuals were more productive. No other variable correlated significantly with productivity (all $P > 0.1$).

To detect whether birds that changed the nest following breeding failure performed better the next year than birds that had also failed, but re-used the same nest-site, we repeated the last two models, but used only cases in which birds failed to produce nestlings during the previous year. Considering only the individuals that failed in the breeding attempt of the previous year, we found that productivity was not affected by nest-site fidelity (GLMM, $P = 0.9$). However, individuals that changed nest showed a significantly poorer breeding outcome than individuals that retained the nest in the next breeding season (0.64 ± 0.06 and 0.96 ± 0.06, respectively; GLIMMIX, $F_{1,56} = 6.75$, $P = 0.011$, *estimate* = −2.8214; model: *scale deviance* = 58.04, $n = 70$).

DISCUSSION

Success or failure, number of nestlings produced during the previous breeding season and age of breeders were found to be correlated with nest-site fidelity in our study population of White Storks, as in other bird species (Rowley 1983, Johannesen *et al.* 2002, Hoover 2003). Younger breeders showed lower nest-site fidelity than adults, statistically corroborating the suggestions made by Schulz (1998).

Variation in nest-site fidelity was explained by age and breeding outcome (success vs. failure) during the previous year. Breeding outcome during the previous year affected nest-site fidelity in some age classes but not in others, for which age seems to be the main influence on an individual's decision to change nest-site. In general, Storks tended to change the nest less often as their age increased. This indicates that experience plays an important role in this behaviour. It is known that young individuals occupy poorer nest-sites in marginal areas and are more prone to fail in breeding. This may account for the lower rates of nest-site fidelity observed in younger individuals. As with other aspects of Stork biology, such as food provisioning (Medina *et al.* 1998), an individual's age determines its experience and therefore its use of resources. Nest-site fidelity can be influenced by an individual's experience, which allows birds better to defend their nests from other less experienced individuals (Prieto 2002). Middle-aged individuals are able to raise their brood successfully, and have the experience necessary to maintain their nest through successive breeding seasons. Nest-site fidelity was also correlated with the productivity of the previous year, although its significance and fitness to models was lower than that observed in models with the breeding outcome of the previous year fitted as a fixed factor. However, the expected decrease in nest-site fidelity in older age classes was not observed. Older individuals have very low rates of breeding failure despite their lower overall productivity (J.I. Aguirre pers. obs.). The significant interaction between sex and productivity of the previous year in relation to nest-site fidelity needs to be analysed in future studies, because too few data have been gathered from our study to draw any conclusions. The significant interaction observed between age and sex in relation to productivity could indicate that the sexes enter the reproductive population at different ages (Prieto 2002), and this behaviour affects nest-site fidelity. This significant interaction might explain the weak differences in nest-site fidelity between sexes and the real effect of the previous year's productivity on nest changes. Younger individuals tend to arrive later in the season (Barbraud & Barbraud 1999) and have to choose among the available nests, finding in many cases that the nest they occupied during the previous breeding season is being defended by another individual. Males tend to arrive before females on the breeding grounds (Barbraud & Barbraud 1999), a fact which could explain the weak sex differences in nest-site fidelity. However, this requires further research.

Nest predation could influence breeding success, as it is the main reason for nestling mortality (Martín 1993, 1995). However, the rarity of predation observed (less than 4% of the nests during the study period, J.I. Aguirre pers. obs.) indicates that this has little effect on breeding success in our population, and therefore on nest-site fidelity. The presence of ectoparasites is known to be another factor that can promote nest changes between breeding seasons (Barclay 1988, Rendel & Verbeek 1996). Nest parasites were not recorded in our study, but ectoparasites at the nest-site have only been observed sporadically in our population (J.I. Aguirre pers. obs.). Changing nest could affect ectoparasite load when the old nest is not occupied for a breeding season, as this may break the parasite cycle. However, few nests in our colonies (less than 5%) are unoccupied in any breeding season, and so the abundance of ectoparasites is not expected to explain significant variation in nest-site fidelity in our population.

In relation to habitat, most of the White Stork's colonies in the province of Madrid are near rubbish dumps, where the birds can find enough food for the entire breeding season (Aguirre & Atienza 2002). As access to resources is similar for all individuals in the colony, we do not expect differences in breeding success to arise from a lack of food. According to our results, coloniality and the size of colony influence neither nest switching rate nor breeding success. For this reason, although the probability of pair switching might increase with colony size (Prieto 2002), this factor has not influenced the aspects studied here. The low predation risk for this population (as above) makes breeding success immune to the effects of colony size, which therefore has no effect on nest fidelity. We found no relationship between habitat and nest-site fidelity because even though the situation of the nests might be different, feeding habitats are similar for both.

Finally, our results show that individuals changing their nest through consecutive breeding seasons have higher breeding failure, even though there were no differences in the number of nestlings produced between pairs remaining at the same nests and pairs changing their nests. These results also occur in Storks that failed in breeding during the previous year. This illustrates the high cost associated with nest changes. In the White Stork, nest changes are usually associated with divorces (Schulz 1998). Mate changes in long-lived iteroparous birds convey costs that have probably arisen from an initial inefficiency of reproducing with a new mate, a reduced reproductive success due to waiting for a new mate, and/or higher rates of mortality or loss of social status (Ens *et al.* 1996, Heg *et al.* 2003). Our findings support these ideas. Individuals suffer from loss of fitness caused by pair change, which can be reflected in a lower breeding success. In the same way, previous experience with the same partner raises breeding success (Pyle *et al.* 2001). Even though these aspects have not been tested in this study (although we identified 19 pairs in which both individuals are of known age, this is insufficient to draw any firm conclusions), they should be addressed in future studies to determine (1) degrees of nest-site and pair fidelity for this species, (2) the fitness costs in cases of divorce and mate fidelity, and (3) whether these costs are equal for both sexes, given that many studies have been able to disentangle the effects of males and females on productivity (Goodburn 1991, Espie *et al.* 2004). We need also to determine the real function of nest changes, rather than just the causes (breeding failure etc.). Monitoring and determining other causes for nest switching such us inter-pair interactions or nest improvement (Prieto 2002) is a challenging task.

We conclude that variation in nest-site fidelity in the White Stork represents an adaptive strategy to increase fitness and therefore can be considered as a defining life-history trait in this species.

We thank the owners and workers of Prado Herrero farm (Soto del Real, Madrid) where most of our data were collected. Manuel Fernández-Cruz, Eva Banda, Javier Marchamalo and Juan Prieto provided data for the analyses. Students of the Faculty of Biology of the Universidad Complutense de Madrid helped during fieldwork. Pilar Baeza improved the English text. Sexing was financed by Guillermo Blanco from the Instituto de Investigación en Recursos Cinegéticos (CSIC). Two anonymous referees substantially improved the manuscript.

REFERENCES

Aguirre, J.I. & Atienza, J.C. 2002. Censo de la Población Reproductora de Cigüeña Blanca (*Ciconia ciconia*) en la Comunidad de Madrid, Año, 2001. In Bermejo, A., de la Puente, J. & Seoane, J. (eds) *Anuario Ornitológico de Madrid. 2001*: 114–125. Madrid: SEO-Monticola.

Akaike, H. 1973. Information theory and an extension of the likelihood principle. In Petrov, B.N. & Csàki, F. (eds) *Proceedings of the Second International Symposium on Interference Theory*: 267–281. Budapest: Akadèmiai Kiadò.

Barbosa, A., Moreno, J., Potti, J. & Merino, S. 1997. Breeding group size, nest position and breeding success in the chinstrap penguin. *Polar Biol.* **18**: 410–414.

Barbraud, C. & Barbraud, J.C. 1999. Is there age assortative mating in the European White Stork? *Waterbirds* **22**: 478–481.

Barbraud, C., Barbraud, J.C. & Barbraud, M. 1999. Population dynamics of the White Stork *Ciconia ciconia* in western France. *Ibis* **141**: 469–479.

Barclay, R.M.R. 1988. Variation in the costs, benefits, and frequency of nest reuse by Barn Swallows (*Hirundo rustica*). *Auk* **105**: 53–60.

Beheler, A.S., Rhodes, O.E. & Weeks, H.P. 2003. Breeding site and mate fidelity in Eastern Phoebes (*Sayornis phoebe*) in Indiana. *Auk* **120**: 990–999.

Blums, P., Nichols, J.D. & Hines, J.E. 2002. Sources of variation in survival and breeding site fidelity in three species of European ducks. *J. Anim. Ecol.* **71**: 438–450.

Bried, J., Pontier, D. & Jouventin, P. 2003. Mate fidelity in monogamous birds: a re-examination of the Procellariiformes. *Anim. Behav.* **65**: 235–246.

Brown, C.R. & Brown, M.B. 1996. *Coloniality in the Cliff Swallow: the Effect of Group Size on Social Behaviour*. Chicago: University Chicago Press.

Burger, J. 1981. A model for the evolution of mixed-species colonies of Ciconiiformes. *Quart. Rev. Biol.* **56**: 143–167.

Carrascal, L.M., Moreno, J. & Amat, J.A. 1995. Nest maintenance and stone theft in the chinstrap penguin (*Pygoscelis antarctica*). 2: Effects of breeding group size. *Polar Biol.* **15**: 541–545.

Cezilly, F., Dubois, F. & Pagel, M. 2000. Is mate fidelity related to site fidelity? A comparative analysis in Ciconiiforms. *Anim. Behav.* **59**: 1143–1152.

Cramp, S. & Simmons, K.E.L. (eds) 1977. *The Birds of the Western Palearctic*, Vol. I. Oxford: Oxford University Press.

Dubois, F., Cezilly, F. & Pagel, M. 1998. Mate fidelity and coloniality in waterbirds: a comparative analysis. *Oecologia* **116**: 433–440.

Ens, B.J., Choudhury, S. & Black, J.M. 1996. Mate fidelity and divorce in monogamous birds. In Black, J.M. (ed.) *Partnerships in Birds: the Study of Monogamy*: 344–401. Oxford: Oxford University Press.

Ens, B.J., Safriel, U.N. & Harris, M.P. 1993. Divorce in the long-lived and monogamous oystercatcher *Haematopus ostralegus*: incompatibility or choosing the better option? *Anim. Behav.* **45**: 1199–1217.

Espie, R.H.M., James, P.C., Oliphant, L.W., Warkentin, I.G. & Lieske, D.J. 2004. Influence of nest-site and individual quality on breeding performance in Merlins *Falco columbarius*. *Ibis* **146**: 623–631.

Forslund, P. & Pärt, T. 1995. Age and reproduction in birds: hypotheses and tests. *Trends Ecol. Evol.* **10**: 374–378.

Fridolfsson, A.-K. & Ellegren, H. 1999. A simple and universal method for molecular sexing of non-ratite birds. *J. Avian Biol.* **30**: 116–121.

Goodburn, S.F. 1991. Territory quality or bird quality? Factors determining breeding success in the Magpie *Pica pica*. *Ibis* **133**: 85–90.

Heg, D., Bruinzeel, L.W. & Ens, B.J. 2003. Fitness consequences of divorce in the oystercatcher, *Haematopus ostralegus*. *Anim. Behav.* **66**: 175–184.

Hoover, J.P. 2003. Decision rules for site fidelity in a migratory bird, the prothonotary warbler. *Ecology* **84**: 416–430.

Johannesen, E., Perriman, L. & Steen, H. 2002. The effect of breeding success on nest and colony fidelity in the Little Penguin (*Eudyptula minor*) in Otago, New Zealand. *Emu* **102**: 241–247.

Jouventin, P. & Bried, J. 2001. The effect of mate choice on speciation in snow petrels. *Anim. Behav.* **62**: 123–132.

Lázaro, E., Chozas, P. & Fernández-Cruz, M. 1986. Demografía de la Cigüeña Blanca (*Ciconia ciconia*) en España. Censo nacional de 1984. *Ardeola* **33**: 131–169.

Littell, R.C., Milliken, G.A., Stroup, W.W. & Wolfinger, R.D. 1996. *SAS System for Mixed Models*. North Carolina, USA: SAS Institute.

Martín, T.E. 1993. Nest predation among vegetation layers and habitat types: revising the dogmas. *Am. Nat.* **141**: 897–913.

Martín, T.E. 1995. Avian life history evolution in relation to nest sites, nest predation and food. *Ecol. Monogr.* **65**: 101–127.

Medina, F.J., Avilés, J.M. & Sánchez, A. 1998. Diferencias intraespecíficas en el uso de un vertedero por parte de la Cigüeña Blanca *Ciconia ciconia* en el Oeste de la Península Ibérica. *Bulletí Del Grup Catalá D'Anillament* **15**: 9–14.

Prieto, J. 2002. *Las Cigüeñas de Alcalá*. Alcalá de Henares: Escuela Taller de Medio Ambiente Albardín. Parque de los Cerros.

Pyle, P., Sydeman, W.J. & Hester, M. 2001. Effects of age, breeding experience, mate fidelity and site fidelity on breeding performance in a declining population of Cassin's auklets. *J. Anim. Ecol.* **70**: 1088–1097.

Reid, J.M., Bignal, E.M., Bignal, S., MacCrackens, D.I. & Monaghan, P. 2003. Age-specific reproductive performance in red-billed choughs *Pyrrhocorax pyrrhocorax*: patterns and processes in a natural population. *J. Anim. Ecol.* **72**: 765–776.

Rendel, W.B. & Verbeek, N.A.M. 1996. Old nest material in nest boxes of Tree Swallows: effects on nest-site choice and nest building. *Auk* **113**: 319–328.

Rowley, I. 1983. Re-mating in birds. In Bateson, P. (ed.) *Mate Choice*: 251–283. London: Cambridge University Press.

Schulz, H. 1998. *BWP Update. The Journal of Birds of the Western Palearctic: White Stork, Vol. 2 Number 2*. Oxford: Oxford University Press.

Sonerud, G.A. & Fjeld, P.E. 1987. Long-term memory in egg predators: an experiment with a Hooded Crow. *Ornis Scand.* **18**: 323–324.

Switzer, P.V. 1993. Site fidelity in predictable and unpredictable habitats. *Evol. Ecol.* **7**: 533–555.

Wittenberg, J.F. & Hunt, G.L. Jr 1985. The adaptive significance of coloniality in birds. *J. Avian Biol.* **8**: 1–78.

Received 25 May 2005; revision accepted 31 January 2006.