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Younger, weaker white stork (*Ciconia ciconia*) nestlings become the best breeders

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ABSTRACT

Background: The literature suggests that migratory bird individuals that hatch first are more fit than their siblings.

Hypothesis: Older siblings in better physical condition will produce more chicks as breeders.

Time and location: A population of white storks nesting in the province of Madrid (central Spain) was monitored annually between 1999 and 2004.

Methods: Hatching order, weight of hatchlings and nestlings, and date of return were recorded and correlated with subsequent fitness and measured as breeding outcome (binomial, failed or successful nests) and productivity (number of nestlings produced).

Conclusions: Contrary to expectations based on their higher nestling weight, and to our hypothesis, first-hatched siblings returned later to the breeding grounds, were less successful, and produced fewer chicks than the rest of the brood.

Keywords: counter-selection, fitness, hatching order, individual decisions.

INTRODUCTION

Evidence that early condition affects long-term fitness has been found in a variety of animal groups, including reptiles (Elphick and Shine, 1998; Clobert *et al.* 2000), birds, and mammals (both reviewed in Lindström, 1999). In birds, it is generally accepted that body condition reached at fledging influences future survival probabilities (Weatherhead and Dufour, 2000; Cam *et al.*, 2003; Brown and Roth, 2004). Sibling competition is one of the most powerful factors explaining intra-brood variation in condition and survival in many species (see reviews in Mock and Parker, 1998; Fargallo *et al.*, 2006). In birds, parents, especially mothers, may manipulate future sibling competition and thereby survival as early as during embryonic development, by differential allocation of resources to eggs according to the laying sequence and/or sex (Slagsvold *et al.*, 1984; Weatherhead, 1985; Bednarz and Hayden, 1991; Gowaty, 1995; Eising *et al.*, 2001; Blanco *et al.*, 2002a, 2002b, 2003). Hatching order influences nestling body condition (Wiebe and Bortolotti, 1994; Kalmbach and Becker, 2005). Older siblings

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often out-compete younger siblings for food and, as a result, grow more quickly (Wiebe and Bortolotti, 1994). Furthermore, after hatching, parents may show skewed food provisioning in relation to chick sex or hatching order within the brood (Lessells, 2002; Ploger and Medieros, 2004), or even direct infanticide (Tortosa and Redondo, 1992; Zielinski, 2002). Nevertheless, younger siblings may also have adaptive growth strategies allowing them to compete with their older siblings (Nilsson and Svensson, 1996). Since brood hierarchy continues after abandoning the nest (Velando, 2000), older siblings will perform better in their first years of reproductive life (Thomas *et al.*, 1999).

Among the consequences of superior early condition is the ability to migrate to feeding grounds in the winter (Cam *et al.*, 2003). This period is particularly critical in migratory species, as the energetic stress of the migratory journey entails an additional risk of mortality (Johnson *et al.*, 2005). The highest mortality rates in birds occur during the first year of life (Schmutz and Fyfe, 1987; Keedwell, 2003; Roth *et al.*, 2005). First-hatched chicks will have lower mortality rates during the migratory journey than the rest of the brood (Cam *et al.*, 2003) due to their better nestling body condition. Therefore, first-hatched siblings are in better condition both as nestlings and as adults and, consequently, higher fitness is expected (Thomas *et al.*, 1999, Cam *et al.*, 2003).

White stork *Ciconia ciconia* is an asynchronous hatching species (see Methods). Hence, it is likely that first-hatched chicks obtain higher body mass as fledglings by using their competitive advantages over their younger siblings throughout the nestling period, as shown in other species (Wiebe and Bortolotti, 1994). The first aim of this study was to confirm this assumption. We also examined whether first-hatched chicks, with presumably better condition at fledging, are also the individuals that arrive earliest at their breeding grounds and nests, taking into account that individuals arriving earlier at the breeding grounds are in better condition than those arriving later (Ninni *et al.*, 2004). Finally, we examined whether first-hatched chicks out-compete their younger siblings and obtain higher breeding success and larger brood sizes during their first years of reproductive life (Thomas *et al.*, 1999). We discuss our results bearing in mind the particular circumstances of food availability of the Iberian white stork populations – that is, the presence of a constant food source throughout the year due to the prevalence of rubbish dumps.

METHODS

Study area and species

The study was carried out on the white stork population of Madrid province between 1999 and 2004 (see Aguirre and Atienza, 2002). The white stork is an asynchronous hatching species with 6 h to 2½ days difference in hatching among chicks (Schulz, 1998). Clutch size and brood size are dependent on individual age (Schulz, 1998), and in the study area (see later) these values are 3.6 (Schulz, 1998) and 2.5 (Aguirre and Atienza, 2002), respectively. Juvenile dispersion was less than 100 km between place of birth and breeding areas (Tortosa *et al.*, 1995; Schulz, 1998).

General procedures

During the study period, a total number of 894 nestlings were marked using metal and PVC rings. Hatching order was assigned by marking the chicks with innocuous ink and applying metallic rings at about 20 days of age. To control for the effect of brood size on hatching order, we categorized hatching order by assigning 1 to the first-hatched chick, 2 to the middle-hatched chick(s), and 3 to the last-hatched chick. Three hundred and thirty nestlings were sexed by molecular procedures (Fridolfsson and Ellegren, 1999) using DNA extracted from blood obtained by brachial vein puncture during PVC banding at an age of 40–50 days. Altogether, 104 of these nestlings were observed copulating in subsequent breeding seasons. We used these data to corroborate DNA sexing. We were able to determine the weight of 45 hatchlings (mean ± standard error: 79.05 ± 1.66) on the day of hatching, and of 330 nestlings of known hatching order, sex, and age during the nestling period (range 19–63 days) using an electronic balance (accuracy 5 g).

Between January and June in 2003 and 2004, we monitored all marked individuals at the colonies to ascertain their arrival date in the breeding areas. In total, we located 135 individuals (79 males and 56 females) of known age (range 2–5 years). In 97 of these individuals, breeding success was monitored. Arrival date was defined as the day of the first observation, with 1 January taking a value of '1'.

From 1999 to 2004, we surveyed 1100 breeding pairs for mark recording. Ninety-four storks (52 males and 42 females) and 165 breeding events were recorded. Marked breeding individuals were between 1 and 5 years old. However, the only one-year old individual was excluded from the analyses, and to balance the data we grouped the 4- and 5-year-old individuals into one class. Hence, we established a total of three age classes. We monitored nests with banded breeders during several visits. Breeding outcome was considered to be a binary variable, where '0' was assigned to failed nests and '1' to successful nests. Productivity was defined as the number of nestlings 40 days after hatching in successful nests (range 1–4). Only one pair produced more than four nestlings. This pair was excluded from the analyses.

Statistical analyses

To examine differences in hatchling mass based on hatching order, we constructed a general linear mixed model (GLMM) using SAS statistical software (SAS Institute Inc., Cary, NC, USA). Such a model allows the use of the nest as a sample unit avoiding problems of pseudoreplication due to the use of the same element within the analysis. As explanatory variables we included sex, hatching order (fixed factors), and laying date (covariate). Nest and breeding year were included as random variables. To determine whether nestling weight was explained by hatching order, we constructed a GLMM in which nestling weight (response variable), sex, laying date, and hatching order (fixed factors) were included. We also included age of nestlings (days) as a covariate to control for this variable. Brood was included as a random factor to control for the difference between first and last fledging from the same nest. Breeding year was also included as a random factor.

To test the effects of hatching order on arrival date at the colony, breeding outcome and productivity as an adult, we used mixed models. When the response variable was binomial (breeding outcome), we applied a generalized linear mixed model (GLIMMIX) with binomial error distribution (Littell *et al.*, 1996); when the response variable was continuous (productivity and arrival date), we applied GLMMs. In these models we included hatching order and sex (fixed factors). Age of breeding adults was included as a covariate because 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). We also included the interaction between sex and hatching order in all models.

When variables did not present a normal distribution (Lillefors $P < 0.05$), we checked the residuals of models. In all cases, except for arrival date, the residuals showed a normal distribution (Lillefors $P > 0.05$), for which the use of GLMMs was suitable. The inverse transformation was used for arrival date (which had a normal distribution), although for descriptive purposes untransformed values are presented in the figures.

We conducted analyses at the population level. They included all data across individual birds within years independent of the number of years that particular individuals were recorded as breeders. In models in which we included data of two or more years from each individual breeder, we considered individual identity as a random factor to avoid pseudoreplication (Hurlbert, 1984). 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 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 greatest 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). We used Akaike's information criterion [AIC (Akaike, 1973)] to determine which model best fit the data. All the analyses were two-tailed.

RESULTS

Hatchling weight was not significantly explained by sex, hatching order or laying date (all $P > 0.4$). On the other hand, nestling weight was significantly explained by sex, laying date, and days of age (GLMM: sex, $F_{1,154} = 5.45$, $P = 0.0208$; days of age, $F_{1,154} = 43.86$, $P < 0.0001$, *estimate* = 26.19; laying date, $F_{1,154} = 25.57$, $P < 0.0001$, *estimate* = −20.76; $n = 330$). Earlier and older males showed greater body mass. Also, nestling weight was only weakly explained by hatching order ($P = 0.1$). The first-hatched chick was the heaviest (mean ± standard error: 3340.29 ± 86.70 g), with only a slight difference between middle (3269.39 ± 86.87 g) and last-hatched chicks (3251.18 ± 86.81 g). *Post-hoc* comparisons showed that there were significant differences between the first- and the last-hatched ($P = 0.0095$) chicks, and near to significant differences between the first- and middle-hatched ($P = 0.072$) chicks. However, we did not observe differences between middle- and last-hatched ($P = 0.353$) chicks. To determine whether hatching first affected nestling weight, we pooled the middle- and last-hatched chicks into one group (hereafter referred to as the 'rest of the brood'). When using this new hatching order (first chick vs. rest of the brood), hatching order did indeed explain nestling weight (GLMM: hatching order, $F_{1,154} = 3.97$, $P = 0.0482$, *estimate* = −78.72). The other explanatory variables remained significant in the model (GLMM: sex, $F_{1,154} = 5.45$, $P = 0.0208$; days of age, $F_{1,154} = 43.86$, $P < 0.0001$, *estimate* = 26.19; laying date, $F_{1,154} = 25.57$, $P < 0.0001$, *estimate* = −20.76; $n = 330$). In the successive models, we used the pooled hatching order assignment (first-hatched vs. the rest of the brood). Moreover, the AIC criterion was always more adequate when including the pooled hatching order than the non-pooled hatching order in the rest of the models.

The mean age of marked breeding individuals was not significantly different between hatching orders in both pooled (ANOVA: $F_{1,164} = 0.47$, $P = 0.493$) and non-pooled aggregations (ANOVA: $F_{2,163} = 0.32$, $P = 0.726$).

Controlling for age of breeding individuals (younger individuals arrive later than older ones), first-hatched chicks arrived later than the rest of the chicks (GLMM: age, $F_{1,52} = 55.80$, $P < 0.0001$, *estimate* = 0.0070; hatching order, $F_{1,52} = 8.39$, $P = 0.0055$; $n = 231$) (Fig. 1). Sex and the interaction between sex and hatching order were not significantly correlated with arrival date (all $P > 0.1$). Also, when we only included individuals with known breeding outcome in the model, first-hatched chicks arrived later than the rest of the chicks (GLMM: age, $F_{1,34} = 15.73$, $P = 0.0004$, *estimate* = 0.0041; hatching order, $F_{1,34} = 4.16$, $P = 0.0492$, *estimate* = 0.0039; $n = 132$).

When controlling for the age of breeding individuals (older individuals are more successful than younger ones), first-hatched chicks were less successful as breeders than the rest of the chicks (GLIMMIX: age, $F_{1,67} = 21.28$, $P < 0.0001$, *estimate* = 1.2907; hatching order, $F_{1,67} = 5.93$, $P = 0.0176$, *estimate* = 0.9526; model, *scale deviance* = 168.71, $n = 165$) (Fig. 2). Sex and the interaction between sex and hatching order were not significantly correlated with breeding outcome (all $P > 0.1$).

Finally, breeding performance, as reflected in productivity, was affected by age and hatching order of the breeding adult. First-hatched chicks showed poorer breeding

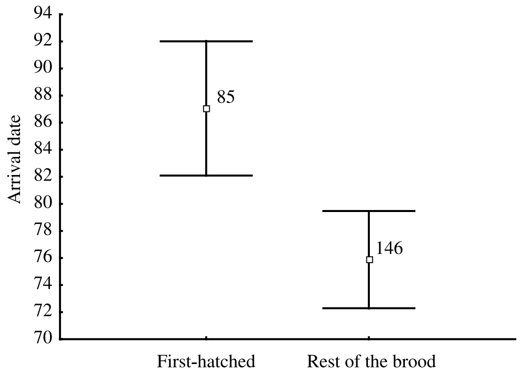

Fig. 1. Differences in arrival date between the first-hatched chick and the rest of the brood. Arrival date: 1 = 1 January. Point and bars represent mean and one standard error. Sample sizes are indicated.

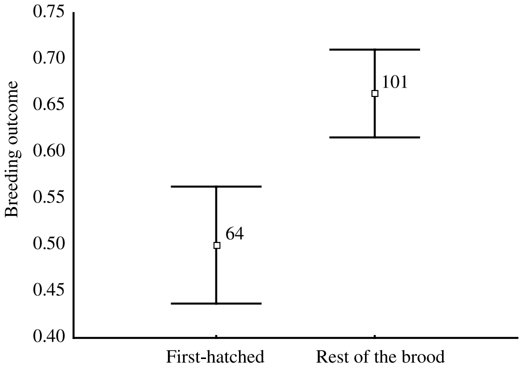

Fig. 2. Differences in breeding outcome between the first-hatched chick and the rest of the brood. Breeding outcome: 1 = successful nests and 0 = failed nest. Point and bars represent mean and one standard error. Sample sizes are indicated.

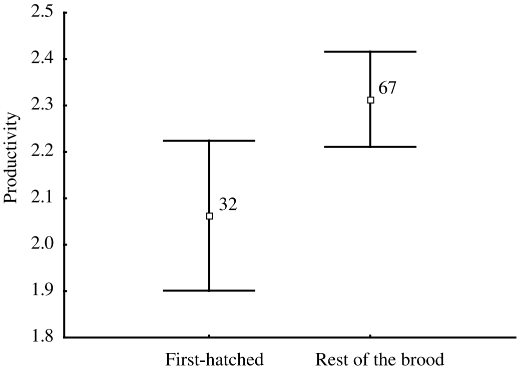

Fig. 3. Differences in productivity (number of nestlings produced) between the first-hatched chick and the rest of the brood. Point and bars represent mean and one standard error. Sample sizes are indicated.

performance later in life and raised fewer chicks per breeding attempt than later-hatched individuals (GLMM: age, $F_{1,27} = 7.45$, $P = 0.011$, $estimate = 0.3987$; hatching order, $F_{1,27} = 4.23$, $P = 0.0494$, $estimate = 0.3807$; $n = 99$) (Fig. 3). Sex and the interaction between sex and hatching order were not significantly correlated with productivity (all $P > 0.1$).

DISCUSSION

To the best of our knowledge, this is the first study to show that younger siblings, apparently with an inferior body condition at fledging, perform better as breeders than their older siblings. As shown for other bird species (Clotfelter *et al.*, 2000; Massemin *et al.*, 2002), white stork hatchlings did not show differences in body mass according to hatching order. However, from the second week, first-hatched chicks reached higher body mass than last-hatched chicks, probably because their larger size gave them a competitive advantage over their siblings (Wiebe and Bortolotti, 1994). This result suggests that hatching first provided these nestlings with a growth advantage. In several species, body mass at fledging was shown to be related to subsequent survival (Krebs, 1999; Clotfelter *et al.*, 2000), and consequently nestling body mass is a fitness-related trait. If first-hatched chicks are favoured by at least a larger body mass over their younger siblings, they are expected to have a better chance of survival. However, an individual's fitness is reflected in its lifetime reproductive success, and it is therefore worthwhile studying long-term effects of nestling traits on reproductive success later in life. Some studies reported long-term effects of nestling body mass, suggesting that higher body mass as a nestling provides an advantage in later years. However, surprisingly, we found that first-hatched white stork nestlings performed worse in their first breeding attempts than later-hatched siblings. The apparent benefit of a larger body mass to first-hatched nestlings was not reflected in breeding success in subsequent years. First-hatched nestlings arrived later at their breeding grounds, failed more often in their early breeding attempts, and when successful breeding was achieved, produced fewer offspring. However, although our results showed that first-hatched nestlings raised fewer chicks per breeding attempt in their first years of life, it is possible that they live longer and, therefore, ultimately balance their life fitness. This requires further research, with complete life histories for each hatching order category to confirm these unexpected results.

A possible explanation for differences in breeding success between hatching order categories might be found in different migratory strategies between young birds. Once fledglings abandon the nest, parental care decreases and fledglings must develop individual strategies to guarantee their own survival and future fitness. One of the strategies to consider is the migratory journey. This journey represents one of the greatest energetic stresses a bird must undergo in its lifetime (Schaub and Jenni, 2001). Later-hatched chicks face a higher probability of failure in the migratory journey, probably because of their lower body mass (Michard *et al.*, 1997). Today, humans supply enriched wintertime environments for storks in the form of rubbish dumps and crayfish-rich (*Procambarus clarkii*) rice fields in the southwest of the Iberian Peninsula (Martínez, 1994; Sánchez *et al.*, 1994; Blanco 1996). Due to this more abundant food supply, younger chicks might actually come to benefit from their initial disadvantage. Their poorer condition at fledging could inhibit them from migrating for some time. During this period of delay, they may enjoy the advantages of the enriched food supply, gaining weight and becoming more able than their older siblings to withstand and survive the rigours of migration, hence arriving earlier at the breeding grounds.

The earlier arrival of later-hatched chicks could result directly in an earlier start to breeding, which has been shown to lead to higher reproductive success (Tryjanowski *et al.*, 2004). On the other hand, earlier arrival also minimizes the time required to search for and occupy a good nest site (Tryjanowski *et al.*, 2004), thereby increasing the time available to accumulate resources, allowing birds to obtain a better physical condition before breeding. Parental physical condition has previously also been shown to influence breeding success in this species (Sasvari and Hegyi, 2001). The latter possibility more likely explains the differences we found in breeding success between first- and later-hatched chicks. Early breeders are probably of better quality, but individuals arriving earlier at the colony are not necessarily so. Food abundance also influences both laying date and brood size (Newton and Marquiss, 1981; Askenmo, 1982; Aparicio, 1994; Tortosa *et al.*, 2003). Natural selection might benefit both early arrivers and early breeders, and their individual condition would help to determine which strategy they choose (Forstmeier, 2002). Even though altering migratory arrival has very high energy costs (Kokko, 1999), sometimes benefits outweigh costs (Forstmeier, 2002). Further studies are needed to test the hypotheses proposed to explain the results of the present study.

Why do first-hatched chicks forego the new food resources and migrate so soon to their traditional wintering sites? It could be that the non-migratory behaviour is evoked by poor body condition rather than by the abundance of food. If the non-migratory behaviour is the selective result of the lesser capability of weaker individuals to face the migratory journey, then, without that selective pressure, the first-hatched chicks would migrate early. If the new abundant food supplies favour a delay in migration, eventually all chicks, including those that hatch first, should evolve to adopt this new pattern. Our results provide the first evidence of individuals in apparently worse body condition at fledging performing better as breeders than the rest of the brood in their first years of life. An analysis of the complete life-histories of individuals is necessary to determine whether the reason for this observation is due to anthropogenic changes. This might be a good example of the human modification of fitness trade-offs.

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