

THE NESTING SYNCHRONISATION PROCESS OF NEW BREEDERS IN A WHITE STORK *CICONIA CICONIA* COLONY

PROCESOS DE SINCRONIZACIÓN DE LOS NUEVOS REPRODUCTORES EN UNA COLONIA DE CIGÜEÑA BLANCA *CICONIA CICONIA*

Xabier CABODEVILLA¹ and Jose I. AGUIRRE¹ *

SUMMARY.—Many studies have focused on the colonial behaviour of birds but information on the processes related to the addition of new breeders to colonies is still scarce. The breeding parameters of new, young, breeders in a colony differ from those of experienced breeders initially. Hence, there must be an underlying process to synchronise such parameters of the new additions to the original colony values. To determine how this synchronisation process takes place, we surveyed a White Stork colony in the northern Madrid province (Spain) for five consecutive breeding seasons. Given the high nest site fidelity of this species, we established a relationship between nest age (new or old) and breeding pair age (young breeder or established adult). Newcomers occupy new nests whereas established breeders use old nests. We compared the laying dates at new nests over a 3-4 year period with those at the old nests in the colony to determine whether new breeding pairs were synchronising their laying dates to those of the existing colony. Young breeders require up to three breeding seasons to synchronise their laying dates with those of the established colony. To our knowledge, this is the first time that such a synchronisation process has been described for storks. Nest age should also be considered when analysing breeding parameters that may differ between young and old breeders.—Cabodevilla, X. & Aguirre, J.I. (2019). The nesting synchronisation process of new breeders in a White Stork *Ciconia ciconia* colony. *Ardeola*, 66: 279-289.

Key words: breeding success, *Ciconia ciconia*, coloniality, colony dynamics, reproduction, synchrony.

RESUMEN.—A lo largo del tiempo, muchos estudios se han centrado en el comportamiento colonial de las aves. Aun así, el conocimiento sobre los procesos relacionados con la incorporación de nuevos reproductores a las colonias sigue siendo escaso. Los parámetros reproductores de las nuevas parejas jóvenes de una colonia son diferentes de los de las aves experimentadas, por lo tanto, debe existir un proceso subyacente para sincronizar dichos parámetros a lo largo del tiempo, entre las parejas jóvenes recién incorporadas y las parejas experimentadas de la colonia. Para determinar cómo se lleva a cabo este proceso de sincronización, se monitorizó una colonia de cigüeña blanca en el norte de la provincia

¹ Departamento de Biodiversidad, Ecología y Evolución. Facultad de Ciencias Biológicas. Universidad Complutense de Madrid, Madrid, Spain.

* Corresponding author: jaguirre@ucm.es

de Madrid (España) durante cinco temporadas de reproducción consecutivas. Debido a la alta fidelidad al sitio de nidificación de esta especie, se estableció una relación entre la edad del nido (nuevo o viejo) y la edad de la pareja reproductora (joven reproductor o adulto). Los reproductores primerizos construyen nuevos nidos mientras que los reproductores experimentados vuelven a usar los mismos nidos de años anteriores. Durante un período de 3-4 años, se comparó la fecha de puesta de los nidos nuevos con la fecha de puesta de los nidos viejos, para determinar si las nuevas parejas reproductoras estaban sincronizando sus fechas de puesta con las aves más experimentadas de la colonia. Nuestros resultados muestran que los reproductores primerizos requieren tres temporadas de cría para sincronizar su fecha de puesta a la de la colonia preexistente. Esta es la primera vez que un proceso de sincronización de la fecha de puesta de nuevos pares de cría se ha descrito en las cigüeñas. La edad del nido también se debe considerar como un rasgo útil en esta especie para analizar varios parámetros de reproducción, que pueden diferir entre reproductores primerizos y experimentados. —Cabodevilla, X. y Aguirre, J.I. (2019). Procesos de sincronización de los nuevos reproductores en una colonia de cigüeña blanca *Ciconia ciconia*. *Ardeola*, 66: 279-289.

Palabras clave: *Ciconia ciconia*, colonialidad, dinámica de colonias, éxito reproductor, reproducción, sincronía.

INTRODUCTION

In the last few decades, many studies have focused on coloniality in birds, proposing different hypotheses regarding its benefits (see Danchin and Wagner, 1997 for review). Such studies centred also on the dynamics of the formation and evolution of colonies, dispersal between breeding seasons and the recruitment of new breeding pairs (Serrano *et al.*, 2004, 2005; Hénaux *et al.*, 2007; Becker, 2015). Little is known, however, about the process by which newcomers to colonies synchronise their laying dates and other reproductive parameters to those of the established colonies over time.

Breeding birds with high pair fidelity often show lower breeding success in their first breeding attempts (Coulson, 1966; Sommerfeld *et al.*, 2015). For example, in a Common Guillemot *Uria aalge* colony, the young breeding pairs that are incorporated into the colony show later breeding dates and lower rates of reproductive success, probably due to their lack of experience (Harris *et al.*, 2016). In line with increased breeding success, synchronisation with the rest of the colony can confer additional benefits of coloniality, arising from reproduction coin-

ciding with the most favorable climatic conditions in the region and periods of greater food abundance in the area, as well enabling young to join premigratory associations of newly fledged chicks.

The White Stork *Ciconia ciconia* is a good model species since it is mainly colonial, especially in southern Europe (Schulz, 1998). It is philopatric, with juvenile nesting dispersion under 50km in most of Europe (Schulz, 1998), and usually exhibits assortative mating (Barbraud and Barbraud, 1999b). Nest site availability at colonies is very low due to high nest site (80%) and breeding pair (83%) fidelity (Schulz, 1998; Barbraud *et al.*, 1999; Vergara *et al.*, 2006). In both cases, fidelity is linked to the age of the breeding pair, with increasing values in older birds, and to the success of the previous breeding season (Schulz, 1998; Vergara *et al.*, 2006; Aguirre, 2009). On the other hand, breeding failures may lead to changes in nest site or breeding partner in the subsequent breeding season (Vergara *et al.*, 2006). Breeding success is also related to the age of the pair and nest site location. Central nests in the colony show lower failure rates (Vergara and Aguirre, 2006) and experienced breeders show higher success than young breeders (Schulz, 1998;

Aguirre, 2009; Fulin *et al.*, 2009). For this reason, young and inexperienced pairs tend to change nesting sites and/or breeding partner more frequently than older individuals (Schulz, 1998; Aguirre, 2009). Older breeders use the same nest over successive seasons, increasing its size annually by adding new materials (Vergara *et al.*, 2010). New breeders must build new nests.

Migration plays a key role in reproduction and colony dynamics since it determines arrival at the breeding grounds. Although the White Stork is traditionally considered a trans-Saharan migrant (Bernis, 1959; Diaz *et al.*, 1996; Schulz, 1998), since the 1990s its migration patterns have shifted and an increasing number of individuals remain to winter in the Iberian Peninsula (Tortosa *et al.*, 1994). The storks' capacity to adjust their migration according to conditions along the route (Gordo *et al.*, 2013), linked to the increasing use of feeding resources at rubbish dumps in Iberia, may be the ultimate reasons underlying these changes in migratory patterns (Tortosa *et al.*, 1995; Flack *et al.*, 2016). Studies using satellite technology reveal that the migration distance of older, more experienced birds is decreasing (Shephard *et al.*, 2015). Young individuals migrate further and over a longer period (Shephard *et al.*, 2015), very often in mixed flocks with more experienced birds: when their migration is solely determined by endogenous signals, it follows a more disoriented pattern (Chernetsov, 2004). This may affect arrival dates at the breeding colonies and thus laying dates. Older individuals arrive earlier at the breeding grounds and start nesting earlier than younger, less experienced, ones (Barbraud and Barbraud, 1999a; Masseurin-challet *et al.*, 2006; Vergara *et al.*, 2007; Gordo *et al.*, 2013).

Given these circumstances, older pairs should occupy the older nests and young breeders should occupy new nests (Vergara and Aguirre, 2006). This being so, old nests

would reflect the breeding parameters of older breeding pairs while new nests would do so for new breeding pairs. Consequently, eventual breeding synchronisation between new, young, breeding pairs and old breeding pairs may be expected over time.

METHODS

The study was carried out at a White Stork colony in northern Madrid province (Spain) (40°44' N, 3°49' E). The colony is in a private Narrow-leaved Ash *Fraxinus angustifolia* dehesa (open woodland with grass understorey). Topped ashes provide an optimal substrate for White Stork nest-building (See Aguirre and Atienza, 2002 for more details of the study area).

All trees were individually labelled each breeding season (1999 to 2003). PVC-marked breeding birds ($n = 30$) were identified, aged and associated with particular nests when they occupied these for at least two weeks prior to breeding. To minimise bias, all direct observations were made by the same field researcher throughout the study period.

During the 2003 breeding season, a detailed study was made of breeding pairs. The following variables were recorded: laying date, laying order, number of eggs laid, hatching date, hatching success, fledging success and nestling biometrics (weight, tarsus length and bill length) prior to fledging (40 days of age ± 10 days). All dates were recorded based on a Julian calendar (1 = January 1st).

Using the regression age = $-5.649 + 0.455$ bill length ($r^2 = 0.906$, $P < 0.0001$), age was estimated for all nestlings with a precision of ± 1 day (Aguirre, 2009). Laying date was calculated by subtracting the mean incubation period (32 days) for the population from the hatching date (Aguirre, 2009).

Between 1999 and 2002 the following parameters were recorded for each nest: laying date, clutch size, and hatching date, as well

as mass (to the nearest 0.5 g), tarsus length and peak length (to the nearest 1 mm) of nestlings when handled during ringing (at between 20-45 days of age). The number of eggs laid in 2002 was not recorded. Laying date was the date the first egg in the clutch was laid. If laying date was not recorded directly, it was determined by backdating using the biometric data of the largest fledgling, with the aforementioned regression. In these cases, the reliability of laying date is subject to the survival of the first eggs.

To test if laying order is related to hatching sequence and the success of the first eggs, 86 breeding pairs in 2003 with known laying and hatching sequences were tested. The fledgling success of nestlings from the first eggs was 91%. We can therefore consider the age of the largest nestling a good indicator of laying date for any particular brood.

This study only used data from successful nests because, between 1999 and 2002, no data from unsuccessful nests were available. In order to standardise data, only successful

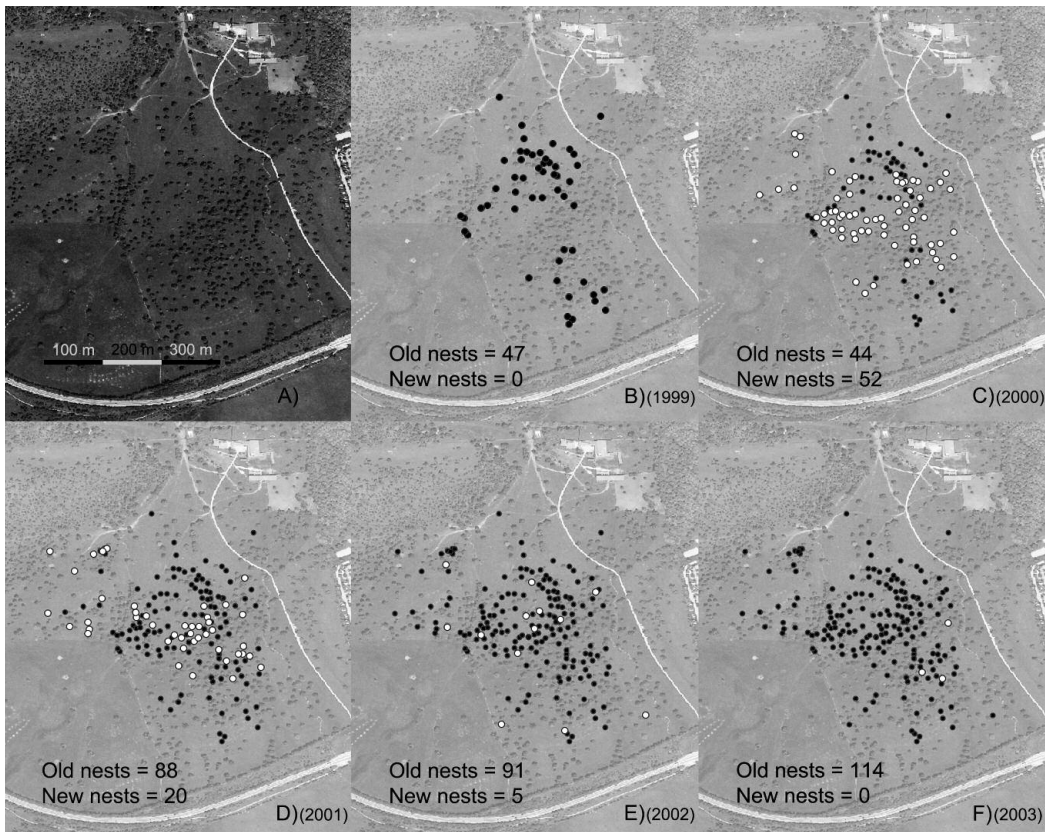


FIG. 1.—Colony growth over the five years of study. For each breeding season, only successful breeding pairs (with at least one fledgling reaching 40 days of age) are written in text. Old nests are displayed as black dots, new nest as white.

[Crecimiento de la colonia a lo largo de los cinco años de estudio. Solo se anotan, en texto, las parejas reproductivas que fueron exitosas en cada temporada de reproducción (en las que al menos un pollo alcanzó los 40 días de edad). Los nidos antiguos se representan en negro y los nidos nuevos en blanco.]

pairs in the 2003 breeding season were considered. During the study period, the number of successful pairs increased from 47 in 1999 to 114 in 2003 (Figure 1). We classified nests into two categories, new and old, based on the period since they had been constructed. We considered as 'old' any nest already built at the beginning of the study in 1999. All nests in 1999 were known to have been present in the colony for at least the previous 3-4 breeding seasons (Aguirre & Vergara, in review). We considered as 'new' any nest built during a given breeding season within our study period. We selected two sets of new nests: those built in 2000, which we termed 'new-1' ($n = 52$) and those built in 2001, which we termed 'new-2' ($n = 20$) (Figure 1).

For every successful breeding pair, laying date, number of fledglings, laying date asynchrony and age of breeders at the time of breeding were recorded. Laying date asynchrony was the number of days between the laying date of a particular new breeding pair relative to the mean laying date of all new pairs for that particular year, or the number of days between the laying date of a particular old breeding pair in relation to the mean laying date of all old breeding pairs for that particular year. Only absolute values were used for laying date asynchrony.

Whenever possible, the age of the known breeders was recorded over the four years of study. Only the first recorded breeding attempt for each breeding pair was included in the analyses to avoid pseudo-replication. Thus, nesting records of the same pair in later years were omitted from the analyses. All observations were categorised under old nests (1999), new-1 (new in 2000) and new-2 (new in 2001).

Prior to 1999, very few individuals were marked and from then on most of the marked individuals were young breeders. This increased the probability of finding marked young breeders. In fact, both in 2002 and in

2003 a two-year-old breeder, two three-year-old breeders and a four-year-old breeder were recorded occupying old nests, probably following the failure or death of an old breeding pair.

To test the age of breeders in every nest category, non-parametric Wilcoxon Rank Sum Tests were performed, due to the small sample size (12 'old' pairs, 11 'new-1' pairs and seven 'new-2' pairs). The three pair categories were compared two by two using breeders' age as a response variable and first year detected as breeders as an independent (grouping) factor.

To test relationships between old and new pairs, laying date, laying date asynchrony, clutch size and number of fledglings were analysed for each age group in each study year (1999, 2000, 2001, 2002 and 2003). The differences in sample size are due to the fact that we used all successful nests and the number of successful nest varied among years for the same group. A series of Mixed Models (using library lme4 in R) were performed. Laying date, laying date asynchrony, clutch size and number of fledglings were used as response variables and first year as breeder as a categorical factor. Year of study was used as a random factor. A series of post-hoc comparisons were performed to test partial significance between different categories (using library emmeans in R). To avoid possible bias related to variance distribution both a more conservative approach (Tukey HSD) and a less restrictive approach (Fisher LSD) were performed. Using only the successful nests in each study year (same N for year; Old = 21; New-1 = 31; New-2 = 11) the same analyses were performed. Under these analyses, very similar results for laying date (Supplementary Material, appendix 1, Figure A1) and the same results for the other studied parameters were obtained. All analyses were performed using R v3.2.5 (R Core Team 2016).

RESULTS

Breeding pairs at old nests were older (mean 5.75 years old, range 2-10 years) than those at new-1 nests (mean 3.55 years, range 2-7) and new-2 nests (mean 2.86 years, range 2-5). No significant differences were found between new-1 and new-2 nests (Supplementary Material, appendix 1, Figure A2). The oldest breeder recorded was ten years of age in 2001, at one of the old nests.

In relation to breeding output, when old and new-1 nests were compared, significant differences were found in 2000 for laying date, laying date asynchrony and brood size but not for fledglings (Table 1). Between 2001 and 2003 significant differences were

only found for laying date in 2001 and only using the Fisher LSD test.

When old and new-2 nests were compared, significant differences were found in 2001 for laying date and in 2002 for laying date and the number of fledglings, but only with the Fisher LSD test (Table 2).

It takes three years for new breeding pairs to synchronise their laying date with the colony laying date according to the Fisher test and two years according the Tukey HSD test (Figure 2). When new nests are built, the mean laying date ranges from 14 to 19 days later than the laying date of old and experienced breeding pairs ($P < 0.001$). In their second year, that difference is reduced to five or six days with significant differences

TABLE 1

Reproductive parameters for new nests in 2000 (new-1) and their evolution over the study years in contrast with old nest (1999) values. Mean (min-max values) values for each parameter are presented. Laying date is given as Julian date (1 = 1 of January). **F, T** = $P < 0.05$ under Fisher LSD and Tukey HSD. **F** = $P < 0.05$ under Fisher but $P > 0.05$ under Tukey HSD. Statistically significant values are represented in bold.

[Parámetros reproductivos de los nidos nuevos del año 2000 (new-1) y su evolución respecto a los valores de los nidos antiguos (1999). Se presenta la media (valor min-max) para cada parámetro. La fecha de puesta se presenta en fecha juliana (1 = 1 de enero). **F, T** = $P < 0,05$ para Fisher LSD y Tukey HSD. **F** = $P < 0,05$ para Fisher LSD, pero $P > 0,05$ para Tukey HSD. En negrita se presentan los valores estadísticamente significativos.]

Year	2000		2001		2002		2003	
Nest category	Old (N=44)	New-1 (N=52)	Old (N=35)	New-1 (N=53)	Old (N=27)	New-1 (N=44)	Old (N=29)	New-1 (N=48)
Laying date (days)	66.48 F,T (52-96)	85.38 F,T (63-134)	61.91 F (52-77)	66.91 F (50-85)	65.78 (55-93)	66.48 (53-83)	69.07 (48-96)	68.54 (51-87)
Laying date asynchrony (days)	5.66 F,T (0.48-29.52)	10.9 F,T (0.62-48.62)	5.73 (0.09-15.09)	6.12 (0.09-8.09)	6.65 (1.22-27.22)	5.09 (0.48-16.52)	7.15 (0.13-27.13)	5.02 (0.46-18.46)
Brood size	4.02 F,T (2-5)	3.38 F,T (1-5)	3.20 (2-4)	3.38 (1-5)	—	—	4.28 (2-6)	4.12 (1-6)
Fledglings	2.36 (1-4)	2.35 (1-5)	3.06 (2-4)	2.89 (1-5)	2.74 (1-4)	2.59 (1-4)	2.69 (1-5)	2.73 (1-5)

according to Fisher tests, but no significant differences according to Tukey HSD tests. No differences were found for laying date in the third year ($P > 0.05$). A fourth year was only tested for new-1 (nests built in 2000) with no significant differences in laying date ($P > 0.05$) found. In 2001 and 2002, significant differences were found in laying date between new-1 and new-2 nests according to the Fisher LSD test, and only in 2001 according to the Tukey HSD test.

DISCUSSION

Our results show the existence of a period during which new pairs gradually synchronise

their laying dates with the colony average. As expected, and in line with previous literature (Vergara *et al.*, 2006), we found a correlation between breeding pair age and nest age: young breeding pairs mainly occupy new nests whilst older breeding pairs occupy older nests. We observed that the old pairs (old nests) have earlier laying dates. The mean age of breeders of the original colony is 5-6 years old, coinciding with the peak of their reproductive life (Aguirre & Vergara, in review).

In new nests, laying date was very much delayed, by 15-20 days, relative to old nests. Young pairs begin breeding later than old pairs, probably because young storks lack experience in nest construction, courtship

TABLE 2

Reproductive parameters for new nests in 2001 (new-2) and their evolution over the study years in contrast with old nest (1999) values. Means (min-max values) for each parameter are listed. Laying date is given as Julian date (1 = 1 of January). **F, T** = $P < 0.05$ under Fisher LSD and Tukey HSD. **F** = $P < 0.05$ under Fisher but $P > 0.05$ under Tukey HSD. Statistically significant values are represented in bold.

[Parámetros reproductivos de los nidos nuevos del año 2001 (new-2) y su evolución respecto a los valores de los nidos antiguos (1999). Se presenta la media (valor min-max) para cada parámetro. La fecha de puesta se presenta en fecha juliana (1 = 1 de enero). **F, T** = $P < 0,05$ para Fisher LSD y Tukey HSD. **F** = $P < 0,05$ para Fisher LSD, pero $P > 0,05$ para Tukey HSD. En negrita se presentan los valores estadísticamente significativos.]

Year	2001		2002		2003	
	Old (N=35)	New-2 (N=20)	Old (N=27)	New-2 (N=20)	Old (N=29)	New-2 (N=28)
Laying date (days)	61.91 F, T (52-77)	75.9 F, T (64-89)	65.78 F (55-93)	72.25 F (61-94)	69.07 (48-96)	68.32 (51-96)
Asynchrony dispersion (days)	5.73 (0.09-15.09)	6.60 (0.1-13.1)	6.65 (1.22-27.22)	5.47 (1.25-21.75)	7.15 (0.13-27.13)	4.97 (0.32-27.68)
Brood size	3.20 (2-4)	3.10 (1-4)	—	—	4.28 (2-6)	3.93 (1-6)
Fledglings	3.06 (2-4)	2.75 (1-4)	2.74 F (1-4)	2.10 F (1-4)	2.69 (1-5)	2.54 (1-4)

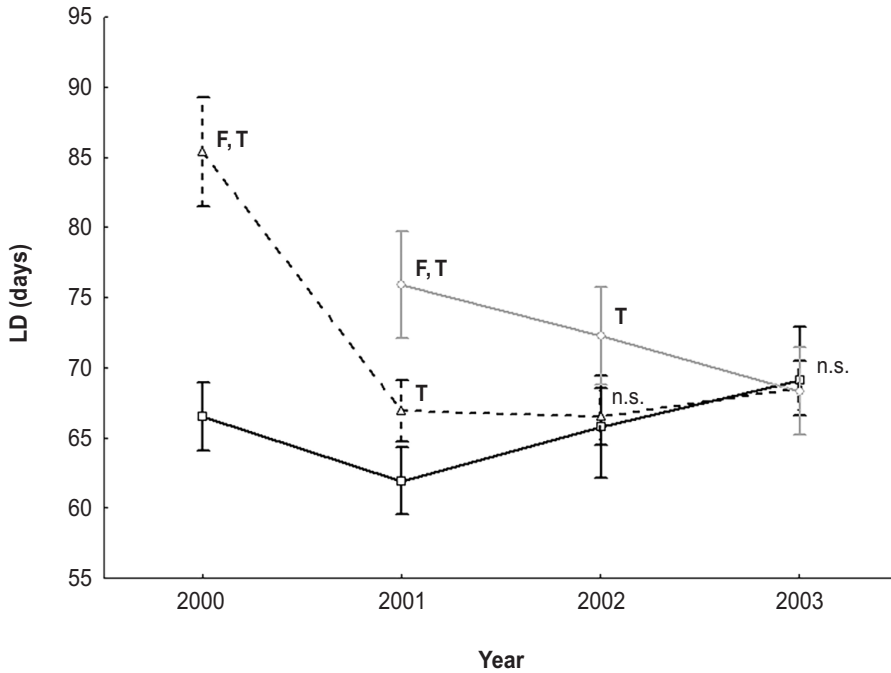


FIG. 2.—Laying date variation between new nests (new-1 and new-2) and old nests over the study. Solid black line represents laying date of old pairs (1999), dotted line represents laying date of new-1 pairs and grey line laying date of new-2 pairs. Symbols are means \pm SE. The *post-hoc* analysis values for comparison between new nests and old nest, for each year, are represented beside the symbols. **F, T** = $P < 0.05$ under Fisher LSD and Tukey HSD. **F** = $P < 0.05$ under Fisher but $P > 0.05$ under Tukey HSD. n.s. = non significant under both approximation methods.

[Variación en la fecha de puesta entre nidos (new-1 and new-2) y nidos antiguos a lo largo del periodo de estudio. La línea continua negra representa la fecha de puesta de las parejas antiguas (1999), la línea discontinua representa la fecha de puesta de las parejas reproductoras new-1 y la línea gris la fecha de puesta de las parejas reproductoras new-2. Los símbolos (los círculos, los triángulos y los cuadrados) representan la media y los bigotes el SE. Los valores de análisis post hoc para la comparación entre nidos nuevos y nidos antiguos, para cada año, se presentan junto a los símbolos. **F, T** = $P < 0,05$ para Fisher LSD y Tukey HSD. **F** = $P < 0,05$ para Fisher LSD, pero $P > 0,05$ en Tukey HSD. n.s. = no significativo para ambos métodos de aproximación.]

and food acquisition (Vergara *et al.*, 2010), and/or because they invest more time in migrating longer distances than old breeding pairs (Shephard *et al.*, 2015). Therefore, environmental conditions that may influence young and old breeders at every stage of the breeding season are also different. Weather conditions or prey availability may determine differential breeding success between

young and old breeders (Tobolka *et al.*, 2015; Eggers *et al.*, 2015). In this particular colony, food availability is constant, since it is located in a very stable environment. Thus, the observed differences are more likely due to the inexperience of young individuals.

In addition, except for the first year of the new-1 nests, no statistically significant differences in laying date asynchrony were

found between new and old nests. This means that both young and adult birds, although they have different initial laying dates, maintain similar asynchrony within their own group, and a similar variance, with a mean difference of ± 5 or 6 days compared to the group average. However, in 2000, a very large influx of new breeding pairs (52 successful new-1 nests), which possibly arrived at different times throughout the breeding season, resulted in high levels of asynchrony. This also explains why the following year this group of nests showed similar asynchrony to the other nests.

The synchronisation of the laying date of new breeding pairs with the existing members of the colony highlights the importance of intra-colony information when colonial birds adjust the timing of their nesting events. It takes up to three years in our model species to synchronise with the rest of the colony, based on a less conservative statistical analysis, and two years according to more conservative statistical approaches. In this particular case, the fact that very few old pairs are using new nests and few new pairs are using old nests increases intra-group variation, giving non-significant differences under the more conservative statistical approach. When we compare the entire series, we show that laying date synchronisation is a gradual process and breeding pairs invest up to three breeding seasons in synchronising their own laying date with that of the colony. Differences found in new nests between first, second and third breeding attempts could be due to: i) the distance and time invested in migration by young breeders, progressively decreasing as they age (Shephard *et al.*, 2015) and/or ii) the experience acquired in the previous year in nest construction, courtship and copulation by young breeders (Vergara *et al.*, 2010).

The fact that we did not account for unsuccessful nests may explain the non-signifi-

cant results for other breeding parameters analysed. As noted by Aguirre (2009), successful young pairs produce more nestlings than old individuals, although the failure rate of young pairs is much higher. The significant differences in clutch size in 2000 and the number of fledglings in 2002 may be due to particular environmental conditions for young pairs nesting later than old pairs. The effect of the weather on nesting success of White Storks is very important (Eggers *et al.*, 2015).

The breeding date synchronisation period between new and older, more experienced, pairs found at this colony may be generally applicable to White Storks and is likely to occur in other colonial bird species. When working with individuals of known age, the age of the nests can be a useful factor in analysing different breeding parameters between young and old individuals of this species. Large sample sizes can contribute to diluting the distorting effect of the few old pairs using newly constructed nests. Failed nests should also be accounted for in future studies.

ACKNOWLEDGEMENTS.—This paper is dedicated to the memory of P. Vergara who collected some of the data for this study. E. Banda and A. Ahtamon helped to improve the early versions of this manuscript. We thank the owners and staff of Prado Herrero farm for their support during the fieldwork. This paper is a contribution to project CGL2017-85637-P of the Spanish Ministry of Economy and Competitiveness.

AUTHOR CONTRIBUTIONS.—Xabier Cabodevilla performed the formal analysis and wrote initial draft of the manuscript. Jose I. Aguirre formulated the research question, provided the study data, he contributed the database and supervised the work. Both authors participated equally in the discussion and preparation on the final version of the manuscript.

REFERENCES

- Aguirre, J.I. (2009). Factores que afectan a la supervivencia juvenil de la cigüeña blanca. Universidad Complutense de Madrid, Servicio de Publicaciones.
- 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*, pp. 114-125. SEO-Monticola, Madrid.
- Barbraud, C., Barbraud, J. & Barbraud, M. (1999). Population dynamics of the White Stork *Ciconia ciconia* in western France. *Ibis*, 141: 469-479.
- Barbraud, C. & Barbraud, J.C. (1999). Is there age assortative mating in the European White Stork? *Waterbirds*, 22: 478-481.
- Becker, P.H. (2015). In search of the gap: temporal and spatial dynamics of settling in natal common tern recruits. *Behav Ecol Sociobiol*, 69: 1415-1427.
- Bernis, F. (1959). La migración de las cigüeñas españolas y de las otras cigüeñas "occidentales". *Ardeola*, 5: 9-80.
- Chernetsov, N. (2004). Migratory orientation of first-year White Storks (*Ciconia ciconia*): inherited information and social interactions. *J Exp Biol*, 207: 937-943.
- Coulson, J.C. (1966). The Influence of the Pair-Bond and Age on the Breeding Biology of the Kittiwake Gull *Rissa tridactyla*. *J. Anim. Ecol.*, 35: 269.
- Danchin, E. & Wagner, R.H. (1997). The evolution of coloniality: the emergence of new perspectives. *Trends Ecol Evol*, 5347: 342-347.
- Díaz, M., Asensio, B. & Tellería, J.L. (1996). *Aves Ibéricas: No passeriformes*. Reyero, J.M. (ed.), Madrid.
- Eggers, U., Arens, M., Firla, M. & Wallschläger, D. (2015). To fledge or not to fledge: factors influencing the number of eggs and the egg-to-fledglings rate in White Storks *Ciconia ciconia* in an agricultural environment. *J. Ornithol.*, 156: 711-723.
- Flack, A., Fiedler, W., Blas, J., Pokrovsky, I., Kaatz, M., Mitropolsky, M., Aghababian, K., Fakriadis, I., Makrigianni, E., Jerzak, L., Azafzaf, H., Feltrup-Azafzaf, C., Rotics, S., Mokotjomela, T.M., Nathan, R. & Wikelski, M. (2016). Costs of migratory decisions: A comparison across eight White Stork populations. *Sci. Adv.*, 2: e1500931-e1500931.
- Fulin, M., Jerzak, L., Sparks, T. & Tryjanowski, P. (2009). Relationship between arrival date, hatching date and breeding success of the White Stork (*Ciconia ciconia*) in Slovakia. *Biologia*, 64: 361.
- Gordo, O., Tryjanowski, P., Kosicki, J.Z. & Fulín, M. (2013). Complex phenological changes and their consequences in the breeding success of a migratory bird, the White Stork *Ciconia ciconia*. *J. Anim. Ecol.*, 82: 1072-1086.
- Harris, M.P., Albon, S.D. & Wanless, S. (2016). Age-related effects on breeding phenology and success of Common Guillemots *Uria aalge* at a North Sea colony. *Bird Study*, 63: 311-318.
- Hénaux, V., Bregnballe, T. & Lebreton, J.D. (2007). Dispersal and recruitment during population growth in a colonial bird, the great cormorant *Phalacrocorax carbo sinensis*. *J. Avian Biol.*, 38: 44-57.
- Massemin-challet, S., Gendner, J., Samtmann, S., Pichegru, L., Wulgue, A. & Le Maho, Y. (2006). The effect of migration strategy and food availability on White Stork *Ciconia ciconia* breeding success. *Ibis*, 148: 503-508.
- R Core Team. (2016). R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. <https://Rproject.org/>.
- Schulz, H. (1998). *Ciconia ciconia*. *BWP Update*, 2: 69-105.
- Serrano, D., Forero, M.G., Donazar J.A. & Tella, J.L. (2004). Dispersal and social attraction affect colony selection and dynamics of lesser kestrels. *Ecology*, 85: 3438-3447.
- Serrano, D., Oro, D. & Ursu, E. (2005). Colony size selection determines adult survival and dispersal preferences: Allee effects in a colonial bird. *Amer. Naturalist*, 166: E22-E31.
- Shephard, J.M., Rycken, S., Almalik, O., Struyf, K. & Van Erp-van der Kooij, L. (2015). Migration strategies revealed by satellite tracking among descendants of a population of European White Stork (*Ciconia ciconia*) reintroduced to Belgium. *J. Ornithol.*, 156: 943-953.

- Sommerfeld, J., Stokes, T. & Baker, G.B. (2015). Breeding success, mate-fidelity and nest-site fidelity in Red-tailed Tropicbirds (*Phaethon rubricauda*) on Christmas Island, Indian Ocean. *Emu*, 115: 214.
- Tobolka, M., Zolnierowicz, K.M. & Reeve, N.F. (2015). The effect of extreme weather events on breeding parameters of the White Stork *Ciconia ciconia*. *Bird Study*, 62: 377-385.
- Tortosa, F.S., Máñez, M. & Barcell, M. (1994). Wintering of White Stork in southwest Spain in 1991 and 1992. *Die Vogelwarte*, 38: 41-45.
- Tortosa, F.S., Pulido, R. & de Reyna, L.A. (1995). Dispersión de juveniles de Cigüeña Blanca (*Ciconia ciconia*) en Córdoba (S de España). *Bulletí del Grup Catalá d'Anellament*, 12: 1-3.
- Vergara, P. & Aguirre, J.I. (2006). Age and breeding success related to nest position in a White Stork *Ciconia ciconia* colony. *Acta Oecologica*, 30: 414-418.
- Vergara, P., Aguirre, J.I., Fargallo, J.A. & Dávila, J.A. (2006). Nest-site fidelity and breeding success in White Stork *Ciconia ciconia*. *Ibis*, 148: 672-677.
- Vergara, P., Aguirre, J.I. & Fernández-Cruz, M. (2007). Arrival date, age and breeding success in White Stork *Ciconia ciconia*. *J. Avian Biol.*: 573-579.
- Vergara, P., Gordo, O. & Aguirre, J.I. (2010). Nest size, nest building behaviour and breeding success in a species with nest reuse: the White Stork *Ciconia ciconia*. *Ann Zool Fennici*, 47: 184-194.

Figure A1: Laying date variation between new successful nests (new-1 and new-2) and old successful nests over the study.

Figure A2: Wilcoxon Rank Sum Tests for breeding pair categories compared two by two for old and new nests (new-1 and new-2).

Submitted: April 04, 2018

Major revision: May 14, 2019

Second version arrives: January 04, 2019

Minor revision: January 05, 2019

Third version arrives: January 08, 2019

Accepted: January 13, 2019

Editor: María del Mar Delgado



© Juan Varela

SUPPLEMENTARY ELECTRONIC MATERIAL

Additional supporting information may be found in the on-line version of this article. See volume 66(2) on www.ardeola.org

SUPPLEMENTARY ELECTRONIC MATERIAL

ARDEOLA, 66(2)

THE NESTING SYNCHRONISATION PROCESS OF NEW
BREEDERS IN A WHITE STORK *CICONIA CICONIA* COLONY

PROCESOS DE SINCRONIZACIÓN DE LOS NUEVOS REPRODUCTORES EN UNA
COLONIA DE CIGÜEÑA BLANCA *CICONIA CICONIA*

Xabier CABODEVILLA¹ and Jose I. AGUIRRE^{1*}

¹ Departamento de Biodiversidad, Ecología y Evolución. Facultad de Ciencias Biológicas. Universidad Complutense de Madrid, Madrid, Spain.

* Corresponding author: jaguirre@ucm.es.

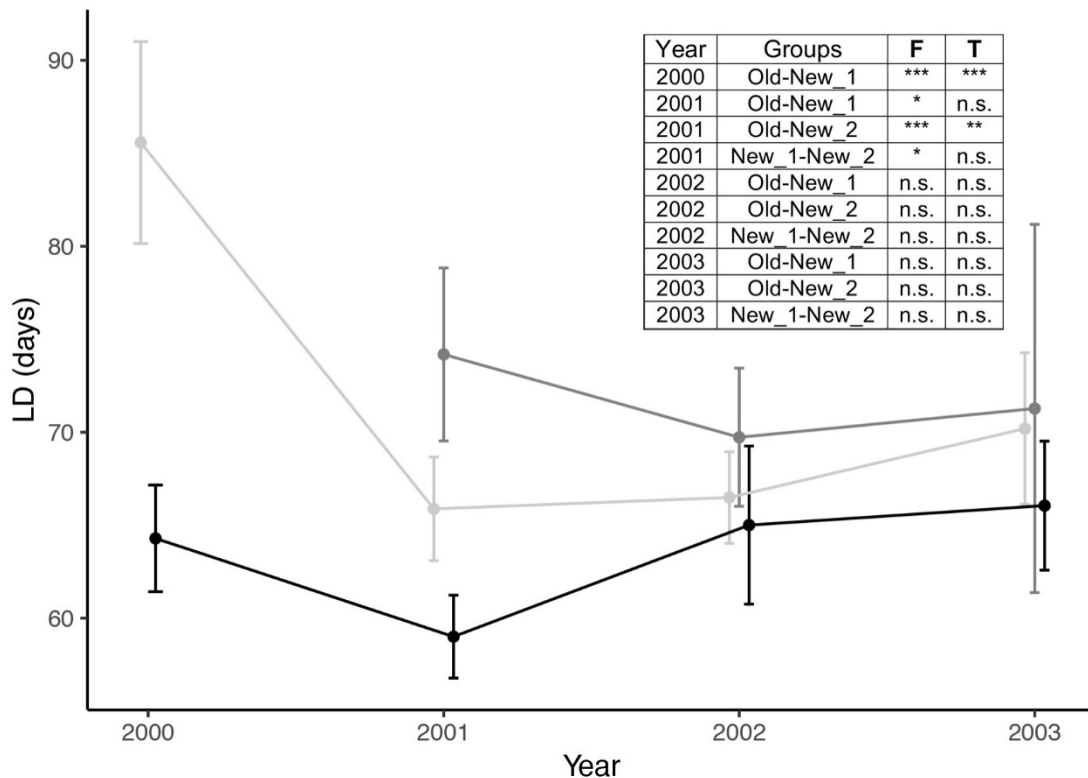


Figure A1: Laying date variation between new successful nests (new-1 and new-2) and old successful nests over the study. Black line represents laying date of old pairs (1999), light grey line represents laying date of new-1 pairs and dark grey line laying date of new-2 breeding pairs. represent means \pm SE. In the upper left corner, a table with *post-hoc* results is inserted. Fisher LSD test is represented by F and Tukey HSD test by T. First column reflects the study years and the second one comparisons between nest groups. *P < 0.05; **P < 0.01; ***P < 0.001; n.s.P > 0.05.

Figura A1: Variación de la fecha de puesta entre los nidos exitosos nuevos (new_1 and new_2) y los nidos exitosos antiguos a lo largo de los años de estudio. La línea negra representa la fecha de puesta de las parejas reproductoras antiguas (1999); la línea gris clara, la fecha de puesta de las nuevas parejas reproductoras new_1, y la línea gris oscura, la fecha de puesta de las parejas de reproductoras new_2. Los símbolos (los círculos, los triángulos y los cuadrados) representan la media y los bigotes el SE. En la esquina superior izquierda, se muestra una tabla con resultados *post-hoc*. La prueba Fisher LSD está representada por F y la prueba Tukey HSD por T. La primera columna refleja los años de estudio, y la segunda la comparación entre grupos de nidos. * P < 0,05; ** P < 0,01; *** P < 0,001; n.s.P > 0,05.

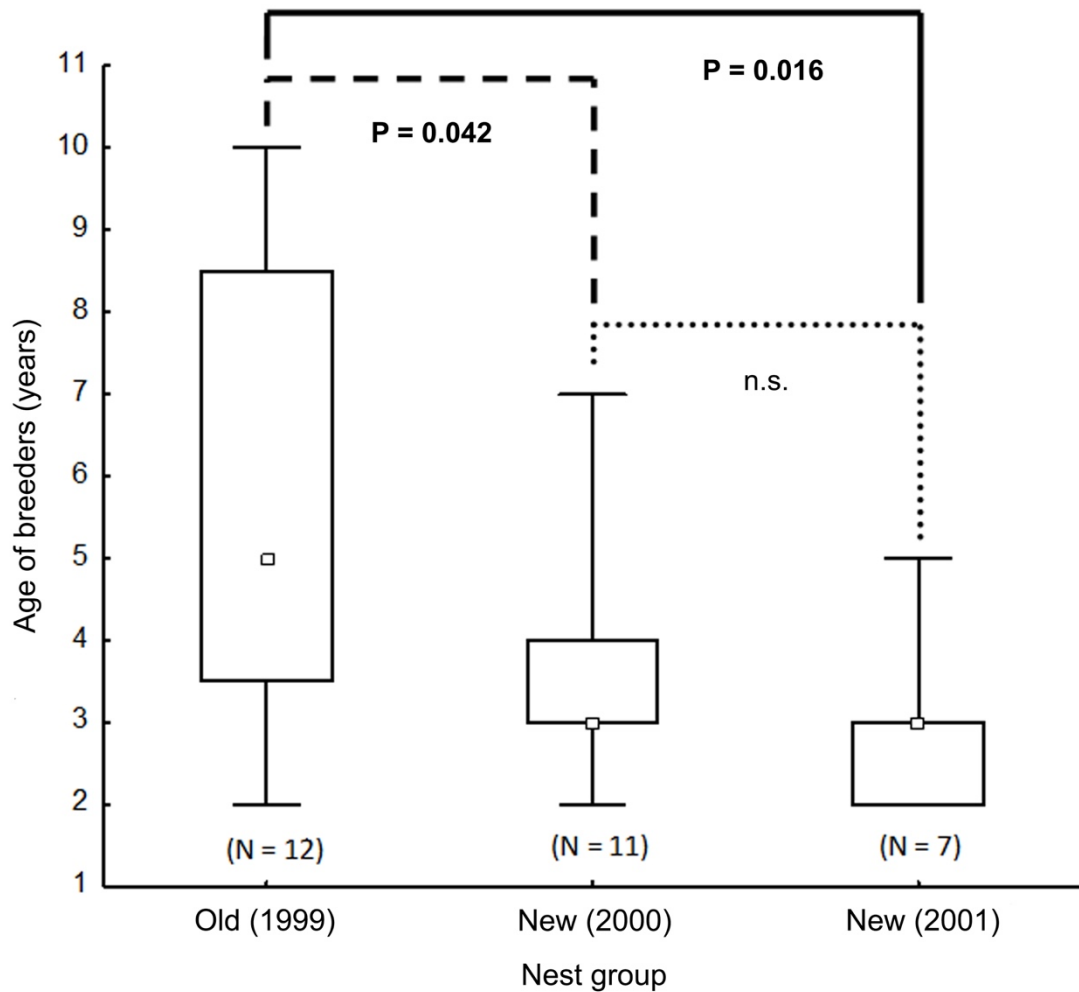


Figure A2: Wilcoxon Rank Sum Tests for breeding pair categories compared two by two for old and new nests (new-1 and new-2). Point represents median, box represents interquartile range and error bars minimum and maximum values.

Figura A2: Pruebas de la suma de rangos de Wilcoxon para edad de las parejas reproductoras en comparaciones de dos entre nidos viejos y nuevos (new_1 y new_2). El punto representa la mediana, la caja representa el rango intercuartil y los bigotes los valores mínimos y máximos.