

Factors affecting growth parameters of White Stork nestlings in eastern Algeria

Naouel Benharzallah · Abdelkrim Si Bachir ·
Fayçal Taleb · Christophe Barbraud

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Abstract Survival and reproduction of young can be affected by growth parameters. It is thus important to estimate intraspecific growth rate variability and environmental factors affecting growth to better understand the dynamics of populations and the potential impacts of environmental changes. Growth parameters of White Stork (*Ciconia ciconia*) nestlings were estimated in eastern Algeria, in the southern part of the species' range. A total of 2,756 measurements of 65 nestlings from 18 nests were taken for body mass, and tarsus, wing and bill lengths. Individual growth data were used to investigate the effects of nest occupation date, laying and hatching dates, clutch size, number of hatchlings, productivity, hatching order, and brood reduction on nestling growth patterns. Body mass and bill length growth rates were lower in the studied population than in a more northerly White Stork population. This supports the hypothesis of a geographic variation in intraspecific growth parameters. Chicks from nests occupied early reached higher asymptotic body mass but tended to grow more slowly. However, chicks from late arriving birds compensated for the difference in body mass

and wing length by higher growth rates. Wing length was significantly affected by asynchrony and hatching order. Last hatched chicks had larger asymptotic wing lengths, lower wing growth rates and longer growth periods. Wings of nestlings from highly asynchronous broods grew faster but took more time to attain the inflection point. Brood reduction had a negative effect on nestling bill length at hatching. Chicks from nests with little brood reduction had a longer bill at hatching than nestlings from nests with high brood reduction.

Keywords *Ciconia ciconia* · Biometry · Breeding parameters · Gompertz model · Growth rate · Logistic model

Zusammenfassung

Einflussfaktoren auf die Wachstumsparameter von im östlichen Algerien brütenden Weißstörchen (*Ciconia ciconia*)

Überleben und Fortpflanzung können von Wachstumsparametern beeinflusst werden. Für ein besseres Verständnis der Dynamik in Populationen und möglicher Auswirkungen von Umweltveränderungen ist es deshalb wichtig, die Variabilität der innerartlichen Wachstumsraten und die das Wachstum beeinflussenden Umweltfaktoren einschätzen zu können. Wachstumsparameter von Nestlingen des Weißstörchs (*Ciconia ciconia*) in Ostalgerien, dem südlichen Teil des Verbreitungsgebietes dieser Art, wurden ermittelt: Zur Bestimmung der Körpermasse sowie der Längen von Schnäbeln, Flügeln und Tarsen wurden 2.756 Messungen an 65 Nestlingen aus 18 Nestern vorgenommen. Der Untersuchung möglicher Effekte auf das Wachstum der geschlüpften Jungen dienten individuelle Wachstumsdaten:

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N. Benharzallah · F. Taleb
Department of Natural and Life Sciences, Faculty of Exact Sciences and Natural and Life Sciences, University Mohamed Khider of Biskra, 07000 Biskra, Algeria

A. Si Bachir
Department of Natural and Life Sciences, Faculty of Sciences, University of El Hadj Lakhdar, 05000 Batna, Algeria

C. Barbraud (✉)
Centre d'Etudes Biologiques de Chizé, UMR7372 CNRS/Univ. La Rochelle, 79360 Villiers-En-Bois, France
e-mail: barbraud@cebc.cnrs.fr

das Datum der Nestbesetzung, des Eierlegens, des Schlüpfens, der Gelegegröße, der Anzahl der geschlüpften Jungen, der Reihenfolge des Schlüpfens und der Brutreduktion. In der von uns untersuchten Population waren die Wachstumsraten von Schnabellängen und Körpermassen geringer als in einer weiter nördlich gelegenen Weißstorch-Population, was die Hypothese einer geographischen Variabilität der innerartlichen Wachstumsparameter unterstützt. Küken von Eltern, die früh bei ihren Nestern ankamen, erzielten höhere asymptotische Körpermassen, zeigten aber eine Tendenz, langsamer zu wachsen. Hingegen kompensierten Küken von spät ankommenden Eltern den Unterschied in Körpermasse und Flügellänge durch eine höhere Wachstumsrate. Asymmetrisches Brüten sowie die Reihenfolge des Schlüpfens hatten eine signifikante Auswirkung auf die Flügellänge. Zuletzt geschlüpfte Küken zeigten größere asymptotische Flügellängen, geringeres Flügelwachstum und insgesamt längere Wachstumsphasen. Die Flügel von Nestlingen aus stark asymmetrischen Brutten wuchsen schneller, brauchten aber länger, um den Wendepunkt zu erreichen. Brutreduktion hatte einen negativen Einfluss auf die Schnabellängen zum Zeitpunkt des Schlüpfens; Küken aus Gelegen mit geringer Brutreduktion hatten zum Zeitpunkt des Schlüpfens längere Schnäbel als Küken aus Nestern mit hoher Brutreduktion.

Introduction

Avian growth and size of nestlings at fledging have important consequences for fitness parameters such as future survival and reproductive success (Gebhardt-Henrich and Richner 1998). Since the notion of fitness is central to evolutionary theory, knowledge of the factors affecting growth rates is fundamental to the understanding of the patterns and evolution of avian growth. Growth rates are often influenced by environmental factors such as food availability (Ricklefs 1983; Martin 1987) or temperature and precipitation (Kosicki and Indykiewicz 2011), and also by intrinsic factors such as brood size, hatching date, clutch size and hatching asynchrony (see review in Richner 1989; Gebhardt-Henrich and Richner 1998). For example, hatching asynchrony, the consequence of birds initiating incubation before clutch completion, affects variation in performance of offspring growth within clutches, which is determined primarily by size hierarchies resulting from asynchronous hatching (Bitton et al. 2006). Generally, last hatched chicks have lower survival probability and/or grow more slowly in weight and tarsus length than first hatched siblings (O'Connor 1978; Ricklefs 1983; Mock 1984).

Nestling development varies between populations of the same species, depending on the particular environmental conditions faced by populations (Barba et al. 1993). At the intraspecific level, growth parameters were found to be affected by geographic variation or time of the nesting season (Ricklefs 1968; Wegrzyn 2012). For example, in the Cape Petrel *Daption capense*, a significant geographical variation in composite growth curves was found between nestlings from different populations (Weidinger 1997). Because survival and reproduction of young can be affected by growth parameters under different environmental factors (Rhymer 1992), it is thus important to estimate intraspecific growth rate variability in different geographic localities if we want to better understand the dynamics of populations and the potential impacts of environmental changes.

The White Stork *Ciconia ciconia* is an asynchronous hatching species (Tryjanowski et al. 2011) that is widespread in the Palearctic and in North Africa with breeding populations occurring from Estonia to southern Morocco (del Hoyo et al. 1992). Body mass and bill length growth of wild nestlings were described by Tsachalidis et al. (2005). Djerdali et al. (2008) studied the effect of parental control over food distribution on nestling body mass at two different sites (southern Spain and northern Algeria) by manipulating broods. More recently, the effects of breeding date and weather conditions on nestling growth rates were investigated by Kosicki and Indykiewicz (2011). However, studies of growth parameters of White Storks have been carried out in central and Eastern Europe and no information is available at lower latitudes, particularly in semi-arid areas. Since clutch size and brood size tend to decrease with decreasing latitude in birds (Ashmole 1963; Ricklefs 1980), one may expect geographical variation in asynchrony and potentially in growth parameters between populations. In addition, earlier studies quantified nestling growth of White Storks using growth data from different nests but few have investigated the effects of hatching asynchrony on growth parameters (Kosicki and Indykiewicz 2011).

The aim of this study was therefore to estimate growth parameters of nestlings in the White Stork in the Constantine region (eastern Algeria, North Africa) within the southern part of the species' breeding range. First, growth data collected according to the age of the nestlings were used in combination to growth models to estimate growth parameters for body mass, and wing, tarsus and bill lengths. Second, individual growth data were used to examine the effects of nest occupation date, laying and hatching dates, clutch size, number of hatchings, productivity, asynchrony, hatching order, and brood reduction on growth parameters.

Methods

Study area and species

The study was conducted during the 2013 reproductive season (January–July) in a White Stork breeding colony located in the farm of Massine (36°19'N, 6°45'E, altitude 736 m), east of Constantine city, in a semi-arid area. The climate is typically Mediterranean with an annual average precipitation of 446.6 mm. The coldest month is February and the warmest month is July (mean temperatures: 6.7 °C and 26.2 °C, respectively). The colony included 20 nests built on walls (6–7 m height) of an abandoned building in a cattle farm. The colony was surrounded by irrigated fields of cereal (durum wheat) and vegetable crops (melons, broad beans).

In Algeria, White Storks most often breed in colonies of an average 11 pairs, but up to 45 pairs (Si Bachir et al. 2012; Moali-Grine et al. 2013). Birds migrate between the end of July and the last decade of August to West Africa south of the Sahara (Jonsson et al. 2006). However, some sedentary individuals were recently observed during the non-breeding period (Moali-Grine et al. 2013).

Data collection

A total of 18 nests were visited daily from January 5 to July 15 (date when the last chick fledged from its nest) to record the following variables for each nest: first occupation date, nest surface area, laying and hatching dates, clutch size, number of hatchlings, productivity, hatching asynchrony and brood reduction.

Nest first occupation date was defined as the first day when an individual was sighted perching or defending an existing nest built during a previous year or constructing a new nest (Vergara et al. 2007). Nest surface area was estimated using the formula $[\pi \times (\text{length}/2) \times (\text{width}/2)]$, where length was the longest measurement on the nest and width was the measurement of its corresponding perpendicular axis (Vergara et al. 2010).

To measure laying date, hatching date, clutch size and number of hatchlings, each nest content was inspected daily using an 8-m-long aluminum ladder. No cases of brood abandonment due to our visits were observed. Laying date was defined as the day on which the first egg was laid. Hatching date was the day when the first chick hatched in the nest. Nest occupation, laying and hatching dates were converted to Julian days (days post-December 31). Clutch size was the number of eggs in the nest when the clutch was complete (Kosicki and Indykiewicz 2011). Clutch completion occurred when the same number of eggs was found during at least five successive nest checks. Eggs were checked daily and numbered with a waterproof felt-

pen on the day they were laid. In White Storks, the average incubation period is 30 days (Schulz 1998). After 28 days of incubation, we inspected nest contents twice a day for signs of hatching. Newly hatched nestlings were marked with nail varnish on their wings and the hatching date of each nestling was defined as its first day of life. Hatching order was expressed as the order of hatching in the brood (1–4). Although a fifth chick was observed in some nests, these chicks were not included in the analyses because they were very few and generally died long before fledging. The number of hatchlings was the number of chicks hatched per nest where eggs were laid.

Productivity was estimated as the number of chicks fledged per nest. Fledged chicks were defined as nestlings older than 7 weeks which were still on the nest and about to fledge (Si Bachir et al. 2012). Brood reduction, the death of one or more chicks through siblicide or starvation (Casado et al. 2008) was expressed as the number of nestlings lost between hatching and fledging. Hatching asynchrony was defined as the period in days during which all eggs hatched (Barba et al. 1993).

The following measurements were taken for each chick every 3 days on average during the growth period from the first day of life to the maximum age of 55 days: body mass was measured with an electronic balance (± 1 g) before 15 days old and with a Pesola spring balance (± 50 g) when older; measurements of bill length, from base of feathers to the tip of upper mandible (± 0.01 mm); tarsus length, from middle of intertarsal joint to distal end of tarsometatarsus (± 0.01 mm); and wing length, the maximum flattened chord excluding the down of young chicks (± 0.01 mm). All measurements were taken using digital calipers. After 35 days, wing length was measured using a graduated rule (± 1 mm).

Modeling growth data

In birds, the most commonly used models to fit growth curves are the Von Bertalanffy, Gompertz and logistic equations (Ricklefs 1983). These models have parameters enabling to make inferences on biological growth processes (Şengül and Kiraz 2005). Here, we opted for the Richards model (Richards 1959) which is one of the most general forms of a family of equations that describe growth from four parameters (Zach et al. 1984). We used the Richards equation $Y_t = A / (1 + \lambda e^{-K(t-T)})^{(1/\lambda)}$ where Y_t is the mass or length measured at age t , A is the asymptotic value (g or mm), t the nestling age (days), K is a constant that determines the curvature of the growth pattern (days^{-1}), T is the inflection point at which the maximum growth rate is achieved (days), and λ is a parameter that designs the curve. If $\lambda = 1$, the Richards equation becomes

the logistic model $Y_t = A/(1 + e^{-K(t-T)})$. If λ tends towards 0, the Richards equation becomes the Gompertz model $Y_t = Ae^{-e^{-K(t-T)}}$. If $\lambda = -1$, the Richards equation becomes the Von Bertalanffy model $Y_t = A(1 - e^{-K(t-T)})$.

A Richards growth curve was fitted to the body mass, tarsus and wing lengths for each individual chick, using a weighed least squares technique and Statistica (StatSoft 2011). The best growth model of each nestling (Gompertz, logistic or Von Bertalanffy) was then selected according to the estimate value of λ (0, 1 or -1). We used the 95 % confidence interval of each λ value to determine whether λ was significantly different from 0, 1 or -1 . Growth models did not converge for some individuals due to insufficient data, so these individuals were excluded ($n = 15$ chicks). Although the Von Bertalanffy model was selected for a few chicks, it did not adequately describe the growth data because of the considerable overestimation of the asymptotic values. We thus used a logistic model for these individuals. As K depends to a certain extent on the quality of fit of the above equations to the data, an independent measure, the time taken to grow from 10 to 90 % (t_{10-90}) of the asymptotic body mass, tarsus and wing lengths, was calculated (Ricklefs 1968).

After visual inspection of the data, it appeared that bill length data plotted against age of the chicks followed a linear pattern. Thus, bill length data were fitted with a linear equation, $BL = bt + a$, where BL is the bill length (mm), t the age of the chick in days and a and b are the linear growth parameters.

We then investigated the effects of nest occupation date, nest surface area, laying and hatching dates, clutch size, number of hatchlings, productivity, asynchrony and brood reduction on the estimated growth parameters of nestlings.

Statistical analyses

First, we conducted Spearman rank correlations between the explanatory variables (nest occupation date, nest surface area, laying and hatching dates, clutch size, number of hatchlings, productivity, asynchrony and brood reduction) that might influence growth parameters to examine collinearity between variables. Because of the high correlations between several covariates (see “Results”), we used a principal component analysis (PCA) to find a small set of linear combinations of the covariates which are uncorrelated with each other and combine the covariates into independent synthetic covariates. Each set is uncorrelated with any other, but components within sets are related (Lezoni and Pritts 1991). This will avoid multicollinearity problems (Donazar and Ceballos 1989) and limit multiple testing issues. The first three components were used in place of the original explanatory variables (see “Results”).

After the PCA ordination, the effect of the synthetic covariates on the growth parameters was tested using generalized linear mixed model (GLMMs) with nest identity as a random effect and including hatching order as a fixed effect in all models. Because multiple tests were performed on the same datasets despite the PCA, we used the Benjamini–Hochberg (BH) procedure to control for false discovery rate (Benjamini and Hochberg 1995). The well-known Bonferroni approach incurs a dramatic loss of statistical power, whereas the BH approach controls well for the false discovery rate with a substantial gain of power. The effect of nest identity (as random variable) was tested by comparing the AIC values between models including or not the nest effect (GLMM and GLM). We concluded that nest identity had an effect on the response variables when the AIC value from a GLM was ≥ 2 points higher than the AIC value from a GLMM (Zuur et al. 2009). Spearman correlations and PCA were conducted using Statistica, while GLMs and GLMMs were performed using the package nlme in R (R Development Core Team 2013). Validation of the fitted models was performed by visualizing normalized residuals and QQ-Plots (Zuur et al. 2009).

Results

Growth patterns

A total of 2,756 measurements were taken on body mass, and tarsus, wing and bill lengths from 65 nestlings. During the nestling period, 16 nestlings died and some could not be measured until 55 days of age being too aggressive to be handled safely. Excluding those nestlings that died early, the mean age when the last measurement was taken was 46 days. The growth of body mass, tarsus and wing lengths appeared non-linear, but appeared linear for bill length. Body mass growth was best fitted with Gompertz models for 53 % of the nestlings and with logistic models for 47 % of the nestling. Tarsus length growth was best modeled with logistic models (89.6 % of nestlings) than with Gompertz models (10.4 % of nestlings). The growth of wing length was best modeled with logistic models for 58 % of the nestlings and with Gompertz models for 42 % of the nestlings (Fig. 1).

Gompertz and logistic models fitted the data very well (mean R^2 for Gompertz, logistic and linear models: 99.4, 99.3, and 99.3, respectively) and there was no effect of rank and the quality of fit (mean R^2 ranged from 98.9 to 99.7).

Parameter estimates indicated higher growth rates (larger K , smaller T and t_{10-90}) for body mass than for wing and tarsus lengths (Table 1). Compared to growth parameters estimated in a White Stork population in Greece,

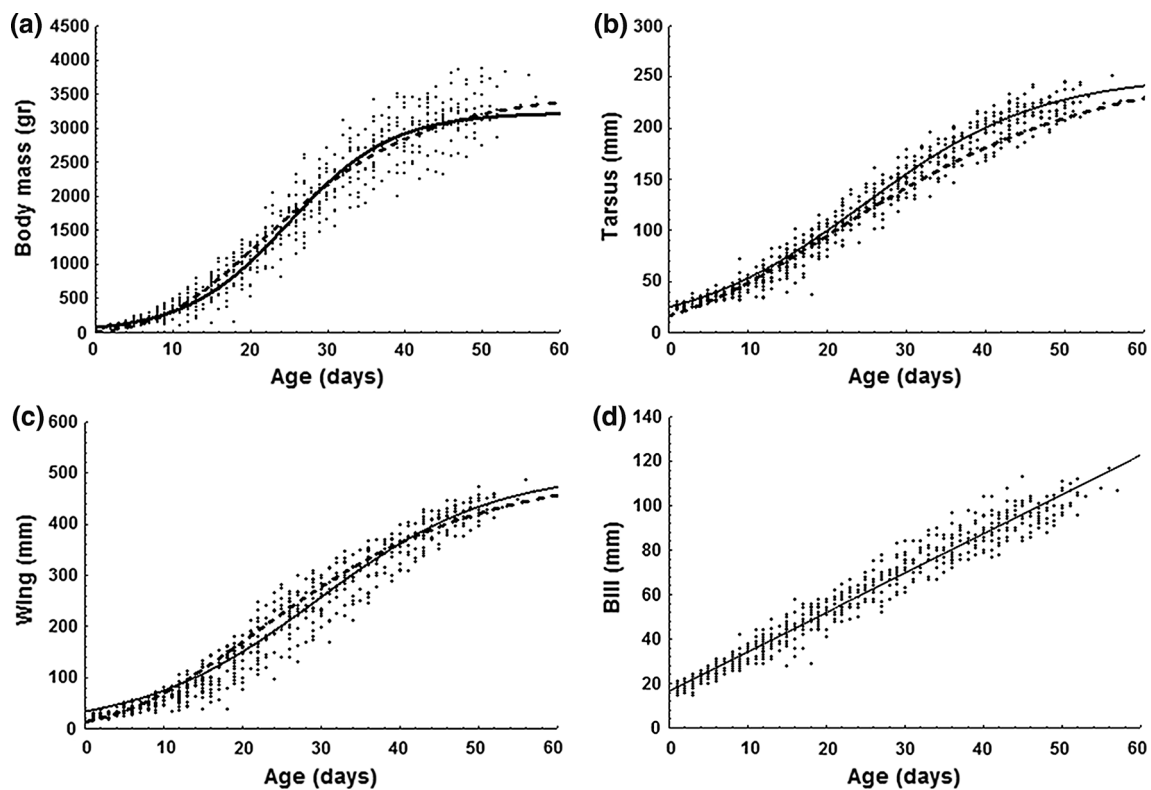


Fig. 1 Measurement data plotted for all chicks as a function of age for White Storks *Ciconia ciconia* in eastern Algeria. **a** Body mass, **b** tarsus length, **c** wing length, **d** bill length. For body mass, tarsus and wing lengths plain lines indicate the fit of logistic models

($R^2 = 0.956, 0.876$ and 0.963 respectively) and *dotted lines* indicate the fit of Gompertz models ($R^2 = 0.957, 0.874$ and 0.964 respectively). For bill length, *plain line* indicates the fit of a linear regression model ($R^2 = 0.964$)

Table 1 Average growth parameters estimated for White Stork *Ciconia ciconia* nestlings in eastern Algeria in 2013 (A13) and Greece in 1997 (G97; Tsachalidis et al. 2005)

Measurement	R^2	A	SE	K	SE	T	SE	t_{10-90}
Mass (g)								
A13	0.99	3396.2	73.8	0.115	0.006	22.9	0.5	34.8
G97	0.97	3436.2	51.7	0.149	0.005	20.6	0.3	29.5
Tarsus length (mm)								
A13	0.99	252.3	2.8	0.080	0.002	24.3	0.4	51.6
Wing length (mm)								
A13	0.99	503.0	5.0	0.070	0.002	26.1	0.7	50.1
Bill length (mm)								
A13	0.99	16.6 ^a	0.4	1.77 ^b	0.02	–	–	–
G97	0.99	19.4 ^a	0.4	2.41 ^b	0.01	–	–	–

R^2 is the coefficient of determination, A is the asymptotic value, K is the growth constant (days^{-1}), T is the age at the inflection point (days), t_{10-90} (days) is the time needed to grow from 10 to 90 % of the asymptotic value

^a and ^b the intercept and slope, respectively, of linear models for bill length

body mass and bill length growth rates were lower in our study population (K_{mass} : $z = 4.353$, $p < 0.001$; T_{mass} : $z = 4.027$, $p < 0.001$; a_{bill} : $z = 5.350$, $p < 0.001$; b_{bill} : $z = 21.952$, $p < 0.001$), but there was no difference in asymptotic body mass ($z = 0.444$, $p = 0.657$) (Table 1).

Combining explanatory variables

Descriptive statistics of the explanatory variables are shown in Table 2. Nest occupation date was positively correlated with laying and hatching dates, but was

Table 2 Mean values and ranges of date of first occupation, nest surface area, laying and hatching dates, clutch size, number of hatchlings, productivity, asynchrony and brood reduction in White Storks recorded in eastern Algeria in 2013

	<i>n</i>	Mean ± SD	Min	Max
Date of first occupation	18	January 16 ± 11.0	January 5	February 10
Nest surface area (m ²)	18	1.61 ± 0.68	0.43	3.06
Laying date	18	March 21 ± 9.6	March 9	April 11
Hatching date	18	April 22 ± 10.0	April 11	May 12
Clutch size	18	4.33 ± 0.59	3	5
Number of hatchlings	18	3.72 ± 0.95	2	5
Productivity	18	2.72 ± 0.75	2	4
Asynchrony (days)	18	4.70 ± 2.50	2	11
Brood reduction	18	1.00 ± 0.67	0	2

Table 3 Spearman rank correlations among variables used to explain variation in growth parameters of nestlings of White Stork during the breeding season 2013 in eastern Algeria (*n* = 18 broods)

	Nest area	Laying date	Clutch size	Hatching date	Number of hatchling	Asynchrony	Productivity	Brood reduction
Nest occupation date	<i>r</i> = −0.83 <i>p</i> < 0.001	<i>r</i> = 0.58 <i>p</i> = 0.012	<i>r</i> = −0.77 <i>p</i> < 0.001	<i>r</i> = 0.55 <i>p</i> = 0.018	<i>r</i> = −0.54 <i>p</i> = 0.021	<i>r</i> = 0.03 <i>p</i> = 0.906	<i>r</i> = −0.28 <i>p</i> = 0.266	<i>r</i> = −0.45 <i>p</i> = 0.064
Nest area	–	<i>r</i> = −0.43 <i>p</i> = 0.072	<i>r</i> = 0.60 <i>p</i> = 0.008	<i>r</i> = −0.42 <i>p</i> = 0.082	<i>r</i> = 0.34 <i>p</i> = 0.166	<i>r</i> = 0.09 <i>p</i> = 0.729	<i>r</i> = 0.21 <i>p</i> = 0.401	<i>r</i> = 0.25 <i>p</i> = 0.327
Laying date	–	–	<i>r</i> = −0.47 <i>p</i> = 0.050	<i>r</i> = 0.99 <i>p</i> < 0.001	<i>r</i> = −0.26 <i>p</i> = 0.291	<i>r</i> = 0.35 <i>p</i> = 0.150	<i>r</i> = 0.02 <i>p</i> = 0.936	<i>r</i> = −0.39 <i>p</i> = 0.109
Clutch size	–	–	–	<i>r</i> = −0.44 <i>p</i> = 0.064	<i>r</i> = 0.69 <i>p</i> = 0.001	<i>r</i> = 0.14 <i>p</i> = 0.579	<i>r</i> = 0.61 <i>p</i> = 0.006	<i>r</i> = 0.29 <i>p</i> = 0.245
Hatching date	–	–	–	–	<i>r</i> = −0.29 <i>p</i> = 0.247	<i>r</i> = 0.30 <i>p</i> = 0.219	<i>r</i> = 0.01 <i>p</i> = 0.969	<i>r</i> = −0.41 <i>p</i> = 0.089
Number of hatchlings	–	–	–	–	–	<i>r</i> = 0.47 <i>p</i> = 0.051	<i>r</i> = 0.70 <i>p</i> = 0.001	<i>r</i> = 0.63 <i>p</i> = 0.005
Asynchrony	–	–	–	–	–	–	<i>r</i> = 0.29 <i>p</i> = 0.241	<i>r</i> = 0.33 <i>p</i> = 0.178
Productivity	–	–	–	–	–	–	–	<i>r</i> = −0.11 <i>p</i> = 0.652

negatively correlated to nest area, clutch size and number of hatchlings (Table 3). Adults that arrived earlier at the colony occupied larger nests, started breeding earlier, laid and hatched more eggs. Clutch size was positively associated with nest surface area, number of hatchlings and productivity. There was no significant relationship between asynchrony and other variables. There was a positive correlation between brood reduction and number of hatchlings. For broods with two hatched chicks, no brood reduction was observed.

The three first axes of the PCA explained 84 % of the variance. These three axes were used as new covariates. The first axis (PC1) accounted for 44.3 % of the variance. Nest occupation and laying dates had high negative (<−0.70) component scores on this axis (Table 4), while nest surface area, clutch size and number of hatchlings had high positive (>0.70) component loadings. Thus, positive

values of PC1 indicated early occupation, early laying (and hatching) dates, large nest surface area, large clutch size, and high number of hatchlings. PC2 accounted for 25.1 % of the variance. A high positive component score (>0.70) was found for asynchrony. Thus, positive values of PC2 indicated asynchronous hatching. Finally, PC3 accounted 14.7 % of the variance and negative values indicated high brood reduction. Although PC2 and PC3 accounted for a relatively low fraction of the total variation, we included them as covariates. Indeed, when using PCA-derived indices, variables that could be of biological importance may not be well accounted for by the first component (the component that contribute the most to total variation). It is thus important to select candidate covariates among the PCs not only based on their contribution to total variation but also in such a way that all original covariates are well represented in the set of candidate covariates.

Table 4 Contribution of nest occupation date, nest surface area, laying and hatching dates, clutch size, number of hatchlings, productivity, hatching asynchrony and brood reduction of White Storks in eastern Algeria to the first three axes of the principal component analysis

	Factors		
	1	2	3
Nest occupation date	-0.905	-0.006	-0.104
Nest area	0.757	0.017	0.209
Laying date	-0.706	0.630	0.077
Hatching date	-0.602	0.679	0.115
Clutch size	0.854	0.306	0.214
Number of hatchlings	0.737	0.535	-0.259
Asynchrony	-0.154	0.777	-0.448
Productivity	0.470	0.641	0.445
Brood reduction	0.464	-0.004	-0.858
Proportion of variance (%)	44.33	25.06	14.70

Factors affecting growth parameters

The growth rate of wing length was affected by hatching order (Table 5; Fig. 2). The second hatched chick was smaller than the oldest nestling, but the difference disappeared gradually during growth (Fig. 2).

For chick body mass, the asymptotic and t_{10-90} estimates were positively related to PC1, while the growth constant was negatively related to PC1 (Table 5). Thus, chicks from nests occupied early (and that hatched earlier) reached higher asymptotic body mass but grew more slowly than chicks from late occupied nests. Although asymptotic body mass tended to decrease with hatching order, the effect of rank was not significant using the BH procedure (Table 5). Second hatched chicks tended to grow faster than first hatched chicks (higher growth constants), but the effect was not significant using the BH procedure. There was no significant effect of PC2, PC3 and nest identity on body mass growth parameters, except for a significant effect of nest identity on the body mass growth constant (Table 7).

Bill length intercept was positively correlated to PC1 while the bill length growth rate tended to be negatively affected by PC1 (Table 5). Thus, nestlings from adults that arrived earlier (and that hatched earlier) had a longer bill at birth but tended to grow slower than chicks from late occupied nests. PC3 had a positive effect on bill length intercept (Table 5) indicating that chicks from nests with little brood reduction had a longer bill than nestlings from nests with high brood reduction. PC2 and hatching order had no effect on bill length growth parameters (Table 5) and there was no evidence for an effect of nest identity on bill length growth parameters (Table 7).

Using the BH procedure none of the variables significantly affected tarsus growth parameters (Table 5).

Nest identity had no effect on tarsus growth parameters (Table 7).

Asymptotic wing length and t_{10-90} estimates were positively affected by hatching order, while the growth constant was negatively related to hatching order (Table 6). The fourth hatched nestlings reached higher asymptotic wing length but grew slower than older nestmates. PC1 had a negative effect on the wing growth constant (Table 6). Chicks from adults that arrived later (and that hatched later) grew faster than nestlings of adults that arrived earlier. PC2 had a positive effect on the wing growth constant and on time at the inflection point (Table 6). Thus, nestlings from highly asynchronous broods grew faster but took more time to attain the inflection point. Nest identity had a significant effect on the wing growth constant and time at the inflection point (Table 7).

Discussion

Breeding and growth parameters

In our study area, first nest occupation dates were much earlier than arrival dates reported in European regions (Barbraud et al. 1999; Ptaszyk et al. 2003; Gordo and Sanz 2008; Fulin et al. 2009; Kosicki 2010). Presumably, White Storks from North African populations arrive earlier on their breeding grounds because migratory distances from wintering areas are shorter compared to the routes followed by European populations (Géroudet 1978; Gordo et al. 2013). We found that early arriving birds occupied larger nests, started breeding earlier and laid more eggs. These findings are in agreement with previous studies in birds which found that early arriving pairs select high quality nests in the most favorable places (Tryjanowski et al. 2004; Si Bachir et al. 2008), start laying eggs earlier and achieve larger clutch size (Vergara et al. 2007; Tryjanowski and Sparks 2008; Fulin et al. 2009). Contrary to some studies in western Poland (Tryjanowski et al. 2004; Tryjanowski and Sparks 2008), but in accordance with others in Spain (Vergara et al. 2007; Gordo et al. 2013) and Slovakia (Fulin et al. 2009), we did not find a negative relationship between nest occupation date and productivity. The link between nest occupation date and productivity can be spatially complex and vary between years (Gordo et al. 2013). Mean clutch size recorded in our study was equal or higher than previously reported in Europe (Tortosa et al. 2003; Profus et al. 2004; Kosicki 2010), suggesting highly favorable feeding conditions in our study area (Tortosa et al. 2003). Brood reduction was positively related to the number of hatchlings with most chicks dying 1–2 weeks after hatching (N.B., unpublished data; Kosicki 2012). Such an increase in nestling mortality with brood size has

Table 5 Results of the generalized linear mixed models testing for the effects of PC1, PC2, PC3 and rank of the nestlings on growth parameters of White Storks of eastern Algeria

	A			K			T			t ₁₀₋₉₀					
	Estimate	SD	p	Estimate	SD	p	Estimate	SD	p	Estimate	SD	p			
	t	t	t	t	t	t	t	t	t	t	t	t			
Body mass (g)															
PC1	151.498	35.996	4.208	<0.001	0.003	-3.650	0.001	0.215	0.253	0.853	0.401	2.273	0.599	3.793	0.001
PC2	-43.619	47.829	-0.911	0.370	0.004	0.343	0.733	0.575	0.333	1.724	0.096	0.461	0.805	0.572	0.571
PC3	-19.215	61.796	-0.310	0.758	0.006	-0.147	0.883	-0.313	0.417	-0.749	0.460	0.326	1.085	0.301	0.765
Rank 2	-151.297	141.442	-1.069	0.294	0.008	2.477	0.020	0.154	1.192	0.129	0.898	-1.751	1.457	-1.201	0.240
Rank 3	-372.987	157.076	-2.374	0.025	0.009	1.489	0.148	-0.009	1.317	-0.007	0.994	-2.810	1.633	-1.720	0.097
Rank 4	-265.804	218.653	-1.215	0.235	0.013	-0.120	0.904	0.537	1.804	0.297	0.768	2.049	2.335	0.877	0.388
Tarsus length (mm)															
PC1	-0.352	0.151	-2.325	0.029	0.001	-1.244	0.225	-0.214	0.220	-0.973	0.340	0.696	0.945	0.736	0.468
PC2	0.149	0.201	0.740	0.466	0.001	-1.483	0.151	0.060	0.293	0.207	0.837	0.994	1.261	0.788	0.438
PC3	0.288	0.241	1.195	0.243	0.001	-2.441	0.022	-0.178	0.352	-0.506	0.616	2.114	1.529	1.381	0.179
Rank 2	0.110	0.678	0.162	0.871	0.001	0.311	0.758	0.841	0.988	0.851	0.403	-1.472	4.049	-0.363	0.719
Rank 3	0.069	0.791	0.087	0.930	0.005	-0.527	0.602	-0.234	1.153	-0.203	0.840	-4.936	4.738	-1.041	0.307
Rank 4	0.797	1.026	0.777	0.444	0.007	-0.114	0.909	4.277	1.494	2.861	0.008	2.201	6.164	0.357	0.724
Wing length (mm)															
PC1	-0.066	0.305	-0.219	0.828	0.001	-3.436	0.002	-0.734	0.405	-1.813	0.084	0.852	0.514	1.656	0.112
PC2	0.100	0.387	0.259	0.798	0.006	3.882	0.001	2.277	0.530	4.294	<0.001	-0.392	0.651	-0.603	0.552
PC3	0.130	0.475	0.275	0.785	0.001	0.565	0.577	0.620	0.689	0.900	0.378	0.726	0.795	0.913	0.371
Rank 2	-0.282	1.055	-0.267	0.791	0.002	-0.614	0.545	0.584	0.979	0.597	0.556	2.427	1.829	1.326	0.198
Rank 3	-0.973	1.202	-0.809	0.427	0.003	-0.057	0.954	0.310	1.118	0.277	0.784	1.093	2.084	0.524	0.605
Rank 4	5.020	1.721	2.915	0.008	0.005	-2.770	0.011	2.558	1.637	1.563	0.133	10.342	2.977	3.474	0.002

p values are uncorrected. Significant *p* values using the Benjamini–Hochberg procedure are shown in bold

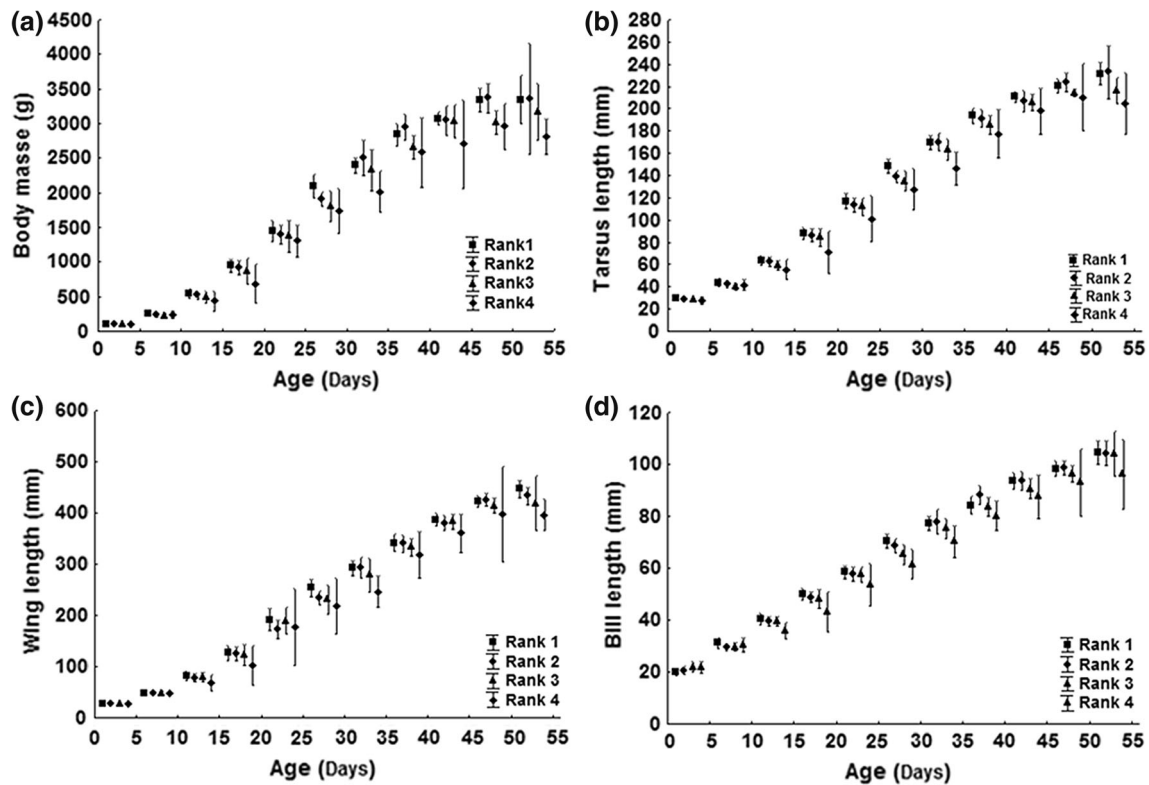


Fig. 2 Mean body mass (a), tarsus length (b), wing length (c) and bill length (d) of first, second, third and fourth hatched chicks calculated at 5-day intervals in eastern Algeria. Errors bars \pm SD

Table 6 Results of the generalized linear mixed models testing for the effects of PC1, PC2, PC3 and rank of the nestlings on growth parameters of White Storks of eastern Algeria

	a				b			
	Estimate	SD	t	p	Estimate	SD	t	p
Bill length (mm)								
PC1	0.057	0.017	3.301	0.003	-0.003	0.001	-2.800	0.009
PC2	0.025	0.023	-1.089	0.286	-0.001	0.001	-0.845	0.405
PC3	0.085	0.030	2.851	0.008	-0.001	0.002	-0.709	0.484
Rank 2	-0.045	0.065	-0.704	0.487	0.001	0.005	0.121	0.904
Rank 3	0.069	0.072	0.957	0.347	-0.008	0.005	-1.519	0.140
Rank 4	0.047	0.101	0.469	0.642	-0.015	0.007	-1.938	0.063

p values are uncorrected. Significant p values using the Benjamini–Hochberg procedure are shown in bold

been observed in several studies (Steidl and Griffin 1990; Viñuela 2000). Brood reduction causes an increase in food intake for the surviving nestlings, and it is generally hypothesized that parents adjust their broods according to their ability to provide food for the nestlings (Dijkstra et al. 1990).

Our results show higher body mass and bill growth rate for nestlings from Greece than for those from Algeria (Table 1; Tsachalidis et al. 2005). This result supports the hypothesis of a geographic variation in intraspecific growth parameters in birds, although other sources of variation

cannot be excluded. Similar results were found between populations of other bird species such as the European Great Tit *Parus major* (Barba et al. 1993) or the Cape petrel (Weidinger 1997). It is suspected that intraspecific geographic growth variation may be related to a combination of climatic variables, food availability and food provisioning rates (Ricklefs 1973; Richner 1989; Rhymer 1992).

Bill growth increased linearly until the age of 55 days. The general shape of the curve suggested that a linear model would be appropriate to describe nestling bill growth. These results are in agreement with those of

Table 7 Testing for the effect of nest identity on growth parameters of White Storks in eastern Algeria

Parameters	GLMM AIC	GLM AIC
Body mass (g)		
<i>A</i>	684.6	683.7
<i>K</i>	−139.1	−131.1
<i>T</i>	269.0	267.0
<i>t</i> _{10–90}	314.6	304.3
Tarsus length (mm)		
<i>A</i>	211.7	209.7
<i>K</i>	−189.2	−191.2
<i>T</i>	242.5	240.5
<i>t</i> _{10–90}	359.4	357.5
Wing length (mm)		
<i>A</i>	234.4	233.4
<i>K</i>	−192.2	−188.1
<i>T</i>	239.2	248.2
<i>t</i> _{10–90}	275.4	274.4
Bill length (mm)		
<i>A</i>	25.2	24.4
<i>B</i>	−195.4	−196.5

GLMM generalized linear mixed model, GLM generalized linear model, AIC Akaike's Information Criterion

Tsachalidis et al. (2005), and suggest that bill growth ended after fledging of the chicks.

Effect of nest occupation date, laying date and nest identity on growth patterns

Overall, our results suggest that chicks from nests occupied early hatched earlier and tended to grow more slowly than chicks from late occupied nests. This was particularly the case for body mass, wing length and bill length, and could be caused by larger brood sizes fed by the parents that bred earlier and which laid larger clutches. Despite slower growth rates, earlier hatched chicks had sufficient time to achieve higher asymptotic body mass than late hatched chicks before leaving the nest. This suggests that birds that arrived earlier had more time to raise their chicks than late arriving ones, and could profit from food abundance at the beginning of the reproductive season to provide more food to their chicks during the entire rearing season. Alternatively, the higher growth rates of chicks from late arriving birds may reflect an increased provisioning effort by the parents which had less time to raise their chicks before the seasonal decrease in food abundance at the onset of summer. A higher growth rate for later hatched chicks has also been reported in the King Penguin *Aptedonytes patagonicus* and in the White Stork (Van Heezik et al. 1993; Tryjanowski et al. 2011). Presumably, more rapid growth in late hatched nestlings permits an earlier nest departure.

The significant effect of nest identity on some growth parameters (body mass and wing growth constant, time at the inflection point of wing growth) may be related to variability in the performance of the parents to provision their chicks. Indeed, since all nests were situated within the same colony and since White Storks forage within a few kilometers from their nest sites (Johst et al. 2001), one can exclude the effect of differences in foraging habitat quality around nests on growth rates.

Effect of hatching order, asynchrony and brood reduction on nestling growth

Only wing length was significantly affected by hatching order, with last hatched chicks showing larger asymptotic wing lengths, lower wing growth rates and longer growth periods. These results are similar to those reported on weight, tarsus and primary feathers growth rates of Egyptian Vultures *Neophron percnopterus* by Donazar and Ceballos (1989): within broods, last hatched chicks grew more slowly in wing lengths than older nestlings. In Black Kites *Milvus migrans*, Hiraldo et al. (1990) suggested that, within the same brood, the last hatched sibling grew slower than its older nestmates. Differences in weight and size between first and last hatched nestlings can be explained by hatching asynchrony. Nestlings that hatched later within nests are in general lighter and smaller than their earlier hatched siblings (Bitton et al. 2006; Węgrzyn 2012). According to Djerdali et al. (2008), breeding White Storks may control intra-brood food distribution which enables parents to invest more in larger siblings under poor environmental conditions. However, our results suggest that body mass of second hatched chicks tended to grow faster than for first hatched chicks, and at the end of the development period there was no difference in asymptotic values except for wing length. Fourth hatched nestlings even reached higher asymptotic wing length (Tryjanowski et al. 2011). Factors not investigated here, such as sex-specific variation in growth rates, may explain this growth variability, and final conclusions cannot be drawn until these factors are assessed.

Within broods, the size hierarchy established by asynchronous hatching increased the mortality of last hatched chicks and caused brood reduction. According to Viñuela (1999), hatching asynchrony is associated with high mortality related to food availability. Brood reduction allows parents to reduce feeding efforts. By raising fewer chicks, parents can provide nestling demands, since brood reduction causes an increase in food intake by the surviving nestlings permitting higher growth rates (Dijkstra et al. 1990). Chicks from nests with little brood reduction had a longer bills at hatching than those from nests with high brood reduction. Since brood reduction was lower in nests

with fewer hatchlings, we speculate that nestlings with initial longer bills were hatched from large eggs (Weidinger 1997). Females may have invested more in egg size than in the number of eggs or may have differed in age or experience (Christians 2002).

To summarize, our study provides the first growth parameters for the White Stork in the southern part of its breeding range. Growth rates were lower than those reported from a more northerly population, suggesting geographic variations. Results indicate that growth rates were influenced by several factors including nest occupation date, laying date, clutch size, hatching asynchrony, brood reduction, nestling rank and nest identity. These findings suggest that these factors must be taken into account in avian growth studies. We also encourage further intraspecific studies on growth rates to quantify the importance and magnitude of geographic variation in growth rates in birds and to decipher the environmental factors causing this variation.

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