



0	Kind to kin: weak interference competition among white stork	53
	<i>Ciconia ciconia</i> broodmates	55
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	Altricial nestlings in structured families show a diverse array of behavioural mechanisms to compete for food, ranging from signalling scrambles to aggressive interference. Rates of filial infanticide are moderately high in white storks. It has been hypothesized that this unusual behaviour is an adaptive parental response to the absence of efficient mechanisms of brood reduction (aggression or direct physical interference) by nestlings. To test this latter assumption, we analyzed video recordings of 41 complete feeding episodes at 32 broods during the first half of the nestling period, when nestlings complete 90% of growth and chick mortality and size asymmetries are highest. Parents delivered food to all nestlings simultaneously by regurgitating on the nest floor. No direct (bill to bill) feeding was recorded. Senior nestlings were never observed to limit their junior nestlings from eating food, either by aggression or physical interference. Experimental feeding tests revealed that heavier nestlings handled prey items more efficiently and ate food at a higher speed. The high degree of tolerance shown by senior nestlings is unusual among birds with similar ecological and phylogenetic affinities, such as herons. Tolerance by seniors cannot be easily explained by absence of parental favouritism or proximate factors known to affect the occurrence of sibling aggression in other species (rate of food transfer, brood size, hatching asynchrony or length of nestling period).	65
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25	In birds and other animals where offspring are fed by parents, food is a limited resource for which nestlings compete, sometimes causing the death of valuable, close genetic relatives (Mock and Parker 1997). Environmental food sources are often scarce and unpredictable (Lack 1947) but much of the competition arising within avian families stems from an initial decision by parents to lay more eggs than the number of chicks they really can raise to independence (Mock and Forbes 1995, Forbes 2007a). Supernumerary chicks are often handicapped by a lower mass or a delayed time at hatching, and the family becomes structured into some ‘core’ and some ‘marginal’ nestlings differing in competitive abilities and, as a consequence, reproductive value (Mock and Forbes 1995, Forbes 2010, 2011).	80
30	Competition among avian nestmates is manifested through a remarkably diverse array of behavioural mechanisms. In most altricial species, competition involves begging displays and jockeying for favourable positions in the nest (Wright and Leonard 2002) resulting in a rather egalitarian distribution of resources where the share obtained by a nestling is mainly dependent upon its intrinsic abilities to beg, jockey or eat the available food (‘scramble’ competition, Nicholson 1954). However, in other bird species with highly structured families, more direct sibling rivalry may ensue (Mock and Forbes 1995, Mock and Parker 1997, Mock 2006). By virtue of their higher mass and developmental head-start, senior nestlings are able to effectively reduce the competitive scope of their junior nestmates and exclude them, total or partially, from meals (Parker et al. 1989, Hudson and Trillmich 2008, Roulin and Dreiss 2012). In this way, the distribution of parental resources becomes skewed, from an almost egalitarian sharing to a despotic distribution (Lomnicki 2009) where the share of resources depends not only upon intrinsic competitive abilities but also on the direct interference caused by other competitors (‘contest’ (Nicholson 1954, Forbes 1993) or ‘interference’ (Mock and Parker 1997, Drummond 2006) competition). Degrees of interference may vary from simply supplanting younger siblings (e.g. jostling, obstructing or pushing them aside when attempting to reach food) to monopolization of current and future meals by establishing an aggressive dominance hierarchy that may end up in the total suppression of a competitor by siblicide (Mock 2006). The degree to which senior nestlings implement and combine different behaviours with varying interference effectiveness is likely to vary both between and within species (Cotton et al. 1999, Roulin 2001, Smiseth and Amundsen 2002, Gonzalez-Voyer et al. 2007).	85
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	The ultimate evolutionary causes and proximate mechanisms underlying this behavioural variation are poorly understood. Most studies have focused on the question of why nestlings in some species are aggressive (Mock and Parker 1997, Drummond 2001a, 2002, 2006, Gonzalez-Voyer et al. 2007), but alternative mechanisms of non-aggressive	90
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0 physical interference still remain almost unexplored, despite
being widespread and causing a considerable bias in food
distribution within broods and differential mortality of some
nestlings (Shaw 1985, Ryder and Manry 1994).

5 While on a broad phylogenetic scale only a minority
of species display sibling aggression (Drummond 2002,
Roulin and Dreiss 2012), it is a highly prevalent trait among
several families of large, long-lived carnivorous birds with
a semialtricial mode of postnatal development (Mock and
Parker 1997, Drummond 2002, 2006). A comparative anal-
10 ysis of 69 species across 7 avian families (Gonzalez-Voyer
et al. 2007) found that the fraction of species showing sibling
aggression in at least half the broods was 27% (spoonbills
and ibises, Threskiornitidae), 54% (egrets and herons,
Ardeidae), 69% (accipiters Accipitridae), and above 90%
15 in boobies (Sulidae), anhingas (Anhingidae) and pelicans
(Pelecanidae). Most species in these groups, both aggressive
and non-aggressive, also show different mechanisms
of physical interference such as food-thieving, supplanting,
obstructing and pushing nestmates aside. Non-aggressive
interference competition is rampant among cormorants and
shags (Phalacrocoracidae; Snow 1960, Olver 1984, Hunt
and Evans 1997), ibises (Skead 1951, Miller and Burger
1978, Ryder and Manry 1994), and herons (North 1963,
Inoue 1985, Jaman et al. 2012).

25 Storks (Ciconiidae) share many ecological and phylo-
genetic affinities with some of these families, particularly
herons and ibises, but they seem to be exceptional in the
sense that nestlings are not aggressive and show little inter-
ference competition (Thomas 1984, Tortosa and Redondo,
1992, Coulter et al. 1999, Klosowski et al. 2002). Storks
may also be exceptional in another aspect of their fam-
ily life. In at least two species (the white and black stork
Ciconia nigra), parents are known to sometimes practice fil-
ial infanticide, directly killing their smallest offspring (Schüz
1943, Haverschmidt 1949, Tortosa and Redondo 1992,
Klosowski et al. 2002, Zielinski 2002). Confirmed cases of
35 filial infanticide in white storks may affect as much as 20%
of breeding pairs (Tortosa and Redondo 1992) and account
for a 30% share of nestling losses due to brood reduction
(Tortosa 1992). In these studies, filial infanticide (a behav-
iour which is rarely reported among birds) has been explained
as a result of nestling storks lacking efficient mechanisms of
sibling rivalry to promote brood reduction, because parents
feed all nestlings simultaneously by regurgitating food on
the nest floor (Tortosa and Redondo 1992, Klosowski et al.
45 2002, Zielinski 2002, Djerdali et al. 2008a). According
to this hypothesis, simultaneous feeding of nestlings with
food dumped on the nest floor makes aggression or virulent
interference by seniors unprofitable because food items are
not economically defendable (Mock 1985, Drummond
2002). This method of indirect parental feeding (i.e. chicks
pick up food from the nest floor) is typical of many storks
but unusual among aggressive species such as herons, where
nestlings often queue to take food directly from the adult's
bill (Mock 1985). When the physical condition of marginal
chicks becomes deteriorated (e.g. by an insufficient food
supply), parents would benefit from a rapid elimination of
marginal nestlings in order not to waste resources in offspring
with low prospective reproductive value. But since senior
60 stork chicks would find virulent interference unprofitable,
they will tolerate the presence of such weakened nestmates,
prompting parents to take the initiative and kill them directly
(Tortosa and Redondo 1992).

Empirical evidence in support of the above hypothesis
is, however, either absent or controversial. Different studies
65 have arrived at opposite conclusions with regard to whether
stork nestlings are aggressive towards their siblings or
capable of interfering with each other for monopolizing food
directly from the parent's bill (Cramp and Simmons 1977,
Tortosa and Redondo 1992, Sasvári et al. 1999a, Klosowski
70 et al. 2002). Other possible mechanisms of non-aggressive
interference competition (e.g. food thieving, obstructing or
supplanting nestmates) have not yet been explored.

White storks are long-lived, monogamous birds that
raise a single brood per year. The modal clutch size is 4 eggs
75 (Cramp and Simmons 1977). Both parents feed chicks with
a huge variety of small prey, predominantly invertebrates
(Tsachalidis and Goutner 2002, Kosicki et al. 2006, Cheriak
et al. 2014). Nestlings attain asymptotic body mass between
45 and 60 d, with maximal growth rates at 20–25 d, and
80 complete 90% of growth during the first 30 d (Tortosa and
Castro 2003, Tsachalidis et al. 2005). Chicks fledge between
70 and 90 d (Redondo et al. 1995, Corbel and Groscolas
2008), becoming nutritionally independent shortly after-
wards. White stork parents make optimistic decisions by
85 laying larger clutches in response to food abundance during
the pre-laying period (Tryjanowski et al. 2005, Djerdali et al.
2008b) but seldom rear as many fledglings as eggs hatched
(Schüz 1943, Haverschmidt 1949), larger clutches suffering
from higher rates of nestling mortality (Massemin-Challet
90 et al. 2006, Benharzallah et al. 2015). White stork broods
hatch asynchronously. Parents begin incubation with the
first or second egg and laying occurs at intervals of two days
(Haverschmidt 1949). Thus, for a modal 4-egg clutch, the
heaviest and youngest nestlings are separated by an average
95 age difference ranging between 2.5 (Tortosa 1992) and
5 d (Kosicki and Indykiewicz 2011). Egg mass also tends to
decrease with laying order (Tortosa and Redondo 1992) and
this effect, combined with hatching asynchrony, results in a
marked size hierarchy among nestmates. Brood asymmetries
100 in size peak between the second and the fourth week of age
(Aguirre and Vergara 2007) and decrease thereafter, both at
nests with and without partial-brood losses (Tortosa 1992,
Djerdali et al. 2008a). Last-hatched nestlings eat a smaller
share of food than their older nestmates (Sasvári et al.
105 1999a), grow more slowly, attain lower asymptotic body
masses (Tortosa and Redondo 1992, Djerdali et al. 2008a,
Benharzallah et al. 2015) and suffer from higher mortality
rates (Tortosa and Redondo 1992, Djerdali et al. 2008a,
Benharzallah et al. 2015). Brood reduction (i.e. differential
110 mortality of late-hatched chicks due to starvation, Mock
1994) accounts for 38% of nestling deaths between
hatching and fledging (Tortosa 1992) and affects 16% of
nests (Kosicki and Indykiewicz 2011). Partial mortality is
heavily accumulated on earlier ages: 91% of deaths occur on
115 nestlings below 20 d of age, 73% concentrating on nestlings
up to 10 d old (Sasvári et al. 1999a, Jovani and Tella 2004).
Much of this mortality is due to climatic adversities such
as low temperatures and rainfall during the earliest part of
the growth period (Kosicki 2012). Very young nestlings are
particularly vulnerable to weather-related mortality due to
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0 the combined effects of a poorly developed thermoregulatory ability (Tortosa and Castro 2003) and the inability of parents to provision sufficient food (Tryjanowski and Kuzniak 2002, Kosicki and Indykiewicz 2011). Consistent with their role as marginal offspring in a structured family, last-hatched
5 white stork nestlings contribute with both insurance and extra components of reproductive value (Mock and Parker 1986), but their value decreases with increasing brood size (Tortosa and Redondo 1992).

10 Our aim in this study was to determine the precise behavioural mechanisms regulating nestling competition in white stork broods during the first 30 d of postnatal development, the critical period when brood asymmetries reach a peak, most mortality occurs and nestling growth is 90% completed. The hypothesis that storks do not show parental favouritism when feeding nestlings was tested by
15 collecting observational data on the timing, distribution, and composition of food from video recordings of natural feeding events. Under parental favouritism, we expected parents to give senior offspring an advantage by feeding
20 nestlings sequentially and/or directly (bill to bill) because older nestlings can reach the parent's bill both sooner and higher (Sasvári et al. 1999a). Also, we expected parents to adjust the size of food items to the size of their heavier offspring because capturing small prey may be less profitable and senior chicks can handle large food items more
25 efficiently (Djerdali et al. 2008a). The hypothesis that stork chicks show little competitive interference during the first half of the nestling period (when growth is 90% complete) was tested by collecting observational data on behavioural mechanisms know to regulate interference competition in other bird species: monopolization of parents' bill, physical
30 obstruction or displacement of nestmates, overt aggression (pecking and threat displays) and non-aggressive disputes over a food item (e.g. food thefts in Roulin et al. 2008). If food disputes were a mechanism of direct interference competition, we expected them to occur more frequently in larger broods where per capita food supply is likely to be lower (Sasvári et al. 1999a, b), to affect junior chicks disproportionately (as victims), to increase the amount of food
35 ingested by chicks initiating or winning disputes, and to be contested (or somehow attempted to be avoided) by victims. Finally, we hypothesized that, in the absence of significant mechanisms of direct interference, scramble competition was the chief mechanism determining competitive asymmetries in white stork broods. To test this hypothesis, we experimentally fed broods a fixed number of items of two food types of the same length: prawns (which nestlings find difficult to handle) and fish (which they can handle easily). We predicted that heavier nestlings were better able to
40 handle difficult prey by virtue of their larger mouth and more advanced motor development and, as a result, they ingested a larger share of the food available to the brood.

45 Our results show that marginal white stork chicks enjoy a peaceful nest life besides their tolerant senior nestmates, who allowed them almost free access to the food provisioned by parents. Cooperative, harmonious sibling interactions are expected on theoretical grounds (Forbes 2007b). Empirical evidence of sibling cooperation is currently accumulating, even in avian taxa where harsh sibling rivalry is notorious (Drummond 2002), such as raptors (Roulin et al. 2012,
50 2016), gulls (Blanc et al. 2010) and ciconiiform wading birds (this study). This remarkable variation within the cooperation-competition continuum in avian families clearly demands an explanation. We use the existing conceptual framework for the evolution of nestmate aggression (Drummond 2002, González-Voyer et al. 2007) to discuss the implications of our findings from an evolutionary perspective.

70 Methods

75 The study was performed during the years 2002–2004 at two different breeding colonies located in Belmez (ca 40 nests in 0.1 km²) and Dos Torres (ca 65 nests in 0.25 km²), Córdoba, Andalusia. Nests are built in holm oaks *Quercus rotundifolia* scattered across a mosaic of pastureland, cereal fields, ponds and meadows. Storks forage both at the surrounding areas of the breeding colonies and at two urban rubbish landfills located several kilometres away.

80 Nests were inspected at least once per week during incubation and every second day around hatching time. Most adults were not ringed and, since we did not perform detailed observations before egg laying, parental sex was unknown. The average hatching span of nestlings within a brood ranged between one and four days. We therefore defined the age of a brood as the age of the oldest chick in days and then established four weekly periods to group nests of a similar age. On each visit, nestlings were weighed with electronic balances (accuracy 1 g). Nestlings within a brood were size-ranked according to their mass (1 = heaviest). Data on individual nestling mass were collected for 67 different broods during the study.

85 During the 2002 breeding season we collected samples of food delivered by parents at 35 nests 1–4 weeks old by using the neck-collar method (Moreby and Stoate 2000, Falk et al. 2006). Cotton-coated wire ligatures were placed around the nestling neck to prevent it swallowing of food, but loose enough not to strangle the chick. After placing neck collars, we monitored nests from a distance with binoculars and as soon as a parent was seen to regurgitate food, we went back to the nest, carefully collected food samples, and removed the collars. Parent storks usually regurgitate a single food bolus on the nest floor containing multiple prey items. Sometimes, the bolus is fractioned in a few portions delivered in a single bout at the same place. The food bolus, therefore, is not divisible, and all chicks pick up prey items from the same food clump. The different prey types were classified into gross categories (e.g. crayfish, earthworms, or insects). Direct observations at nests suggested that small chicks may find it difficult to handle and swallow large food items (see also Djerdali et al. 2008a). We were interested in testing whether parents either promoted or disfavoured nestling competition by delivering food items that could be either monopolized by senior nestlings (Djerdali et al. 2008a, b) or accessible to the smallest chicks in a brood. Therefore, we measured the length of the largest food item (to the nearest mm) as a proxy for prey size that could be limiting for smaller chicks.

90 During the spring 2002, we also performed a pilot study to gather background information about nest accessibility and bird behaviour in order to improve techniques for
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0 nestling identification and video recording. This pilot study
 included recordings at 15 broods 1–6 weeks old but these
 were not included in the analysed sample.

5 **Observations of natural feeding events**

Continuous samples of parent and chick behaviour were
 collected at nests during the 2003–2004 breeding seasons.
 We placed video cameras (8XR, SONY CCD-TR617)
 attached to a universal bracket fixed to an aluminium pole
 10 2.5 m long, which was fastened to tree branches by sev-
 eral anti-slip straps provided with buckles. This allowed
 the camera to be adapted to a variety of nest-tree structures
 in order to film broods from a distance of 1.5–2 m at an
 inclination angle of ca 45°–60° from above. Before plac-
 15 ing the recording device, we observed parent storks to land
 on nests from a distance with the help of binoculars, in
 order to not interfere with their preferred landing positions.
 Neither parents that landed on the nest nor chicks showed
 any visible signs of disturbance in response to cameras. Prior
 20 to recording sessions, nestlings were individually marked on
 the head and shoulders with a unique colour code using
 non-toxic acrylic paints. Camera batteries had an autonomy
 of about 2.5 h, which allowed to record one or two feed-
 ing events per nest at the most. Out of 444 h of video, we
 25 recorded 62 parental visits at nests, of which 47 visits at 34
 different nests (155 h) included parents regurgitating food.

Despite we attempted to obtain a balanced sampling
 design where each nest and age block (week) was represented
 by an equal number of observations, this proved impossible
 30 due to logistic complications. Some video sequences were
 unsuitable for measuring certain variables at feeding events,
 because either parents or chicks obstructed the visual field.
 The final useful sample size was 41 feeding episodes at 32
 nests containing 2–5 chicks aged 1 to 4 weeks.

35 We measured the latency (to the nearest 0.1 s) of parents
 to deliver food as the time since an adult landed on the nest
 until it disgorged food. After a parent landed on the nest,
 chicks began to walk approaching it until they stopped
 forming a circle beneath the parent's head. White stork
 40 nests are remarkably large (80–150 cm diameter on aver-
 age, but may reach up to 250 cm, Cramp and Simmons
 1977), allowing plenty of space for young nestlings to
 waddle slowly around the nest platform. The total duration
 of nestlings approaching parents and forming a circle prior
 45 to feeding was measured as the time since the first nest-
 ling got up until the last nestling stopped walking at the
 circle. The duration of food consumption by nestlings was
 measured as the time since parents began to disgorge food
 until all nestlings had ended swallowing. In addition, we
 50 measured occurrences of some specific behaviours poten-
 tially involved in sibling competition in this and other
 species:

1) Aggression. Older nestlings are capable of throwing
 pecks at other family members (Redondo et al. 1995,
 55 Sasvári et al. 1999a). We also looked for other (non-pecking)
 possible forms of sibling aggression or intimidation, e.g.
 pushing, shagging or dragging (Braun and Hunt 1983),
 forced immobilization of junior chicks (Medeiros et al.
 2000), or threat displays (e.g. as in painted storks *Mycteria*
 60 *leucocephala*, Urfi 2011). We recorded the occurrence of
 aggressive behaviours and the identity of aggressors and
 victims.

2) Monopolization of the adult's bill. Following Mock
 (1985) and Parker et al. (1989), scissoring was defined as
 65 any grip of the parent's bill preceding food regurgitation.
 We computed scissoring rates for individual nestlings as the
 number of bill-to-bill contacts divided by the time that the
 adult's bill was within reaching distance of the chicks, before
 food was regurgitated. Most scissoring bouts consisted of
 70 intermittently gripping and sliding on the parent's bill but
 some nestlings grasped it firmly or attempted to insert their
 bill into the parent's. Because preferential access to the
 parent's bill in the event of food regurgitation might give
 heavier chicks a competitive advantage (Mock 1985), we
 75 recorded whether grasping resulted in direct feeding. A food
 bolus was considered direct if a nestling swallowed it before
 reaching the nest floor and indirect otherwise (Mock 1985).

3) Obstructing and supplanting nestmates. Nestlings,
 particularly larger ones, could potentially prevent their
 nestmates from eating food by supplanting or pushing
 80 them aside, as in ibises (Skead 1951, Herring et al. 2010)
 and jabiru storks *Jabiru mycteria* (J. Villarreal-Orias pers.
 comm.), or by obstructing their access to the regurgitated
 food. White stork chicks conspicuously stretch and wave
 their wings while eating food. In the African openbill stork
 85 *Anastomus lamelligerus* nestlings prevent others from eating
 food by opening wings (Kahl 1972a). We recorded whether
 nestlings, independently of their size, were obstructed,
 supplanted or pushed aside by a nestmate during feeding
 events.

4) Food disputes. Dyadic interactions between chicks
 over a single food item occurred either because two nest-
 90 lings seized the same piece at the same time, both pulling
 simultaneously until one nestling finally released it (tug-
 of-war, Mock 1985), or because a nestling (the receiver),
 while attempting to swallow a large food item was 'assaulted'
 95 by a nestmate (the actor) who also grasped the same item
 (described as 'thefts' in Medeiros et al. 2000 and Roulin
 et al. 2008). Food disputes did not involve any aggression,
 just pulling apart or swallow attempts of the same food item
 100 by two nestlings simultaneously. Food disputes might give
 heavier chicks a competitive advantage, as in hen harriers
Circus cyaneus (Balfour and Macdonald 1970) and barn owls
Tyto alba (Roulin et al. 2008). Tug-of-war interactions have
 also been reported in lesser adjutant stork *Leptoptilos javanicus*
 105 nestlings (Maust et al. 2007). We recorded the identity of
 the participants as well as the outcome of the dispute. A
 nestling was assumed to win a dispute if it ended swallow-
 ing the food item and to lose it if the food was eaten by
 its opponent. In the case of food assaults, we also recorded
 110 any behaviour by receivers to avoid being robbed, such
 as concealing food, attempting to hide from the actor, or
 performing communicative displays (Roulin et al. 2008,
 Dreiss et al. 2016).

Observations of filmed natural feeding events allowed a
 115 gross estimate of rates of food intake by nestlings, defined as
 the number of food items ingested. A food item was defined
 as the fraction of the bolus handled and finally swallowed
 by an individual chick. Data from video recordings allowed
 determining the composition of 40 feedings at 28 different
 120 nests (for the validity of this method see Hampfl et al. 2005

0	and Dolata 2006). Classification of prey types was based on information on nestling diet collected by the neck-collar method during the 2002 breeding season.		
	Observations of experimental feeding events		
5	Preliminary observations suggested that handling time of food items varied according to the type of individual prey that made up the food bolus, being longest when nestlings attempted to swallow large crayfish <i>Procambarus clarkii</i> .		
10	Since food items in natural feeding events may vary in size and handling difficulty, this complicated estimating food intake rates at natural nests. Therefore, we designed an experimental setup to determine how nestling mass affected rates of food intake and handling time under more controlled conditions.		
15	At 26 nests (12 in 2003 and 14 in 2004) containing 2–5 chicks, we provided nestlings with two types of food items of the same size (7–8 cm length), namely fish (<i>Engraulis</i> sp.) and prawns (<i>Parapenaeus</i> sp.), which are easy and difficult to be handled by nestlings, respectively. The two food types were presented in two separate tests 24 h apart, in randomly alternating order. The number of items was twice the size of the brood. We selected only broods in their second week to minimize age variations. This age was chosen because nestlings had attained a good degree of sensory-motor development but they still lacked immobilization responses in the presence of humans, a behaviour which typically appears on the third week after hatching.		
20	We climbed to the nest, attached the video camera, weighed and marked chicks and placed them in a semicircle before presenting the food in front of them. At nests where parents had recently fed, tests were delayed for 1 h (2–3 chicks) or 1.5 h (4–5 chicks), to ensure that all broods were sufficiently hungry. These periods were established according to natural feeding intervals at this age (Tortosa 1992). We then came down the nest-tree and allowed chicks to eat the food for a 30 min period. From video recordings of experimental feeding events, we recorded the number of food items selected and swallowed by each nestling and whether nestlings engaged in any form of physical interference or a food dispute. Handling time was measured as the interval from first bill contact to the completion of swallowing (Mock 1985).		
25	Human presence and climbing to the nests reduced the time spent by adults brooding nestlings, so we avoided visiting the colony during rainy weather and the central hours in hot days. No nest was abandoned but four nestlings died during the study. Three of them were the smallest chicks in their brood and apparently died of starvation. One second-largest chick also died, apparently from choking or suffocation. Our sampling procedure, however, precluded any accurate estimation of mortality rates because not all nests were monitored until four weeks old and thus some instances of nestling mortality may have gone undetected.		
30	Nests were revisited at 45–50 d to ring nestlings.		
	Statistical analyses		
35	Statistical analyses were performed in R (R Core Team). To account for lack of statistical independence (Hurlbert		
40	1984) among nestlings belonging to the same brood, we performed linear mixed-effects models LMM by using the package ‘lme4’ (Bates et al. 2014) with nest and chick as random factors. P values for F tests were computed by Kenward–Roger approximation of degrees of freedom by using the package ‘afex’ (Singmann et al. 2015). As a result of haphazard sampling (Quinn and Keough 2002) of natural feeding events, the final dataset was incomplete, in the sense that the number of samples was higher than the number of nests, and unbalanced with respect to brood age. When Kenward–Roger approximation failed due to an unbalanced design, signification of fixed effects was tested by Wald chi squared tests (Bates et al. 2014). For every model, we visually checked for homoscedasticity (residuals vs fitted plots) and normality of residuals (normal quantile plots) (Quinn and Keough 2002). Some variables (nestling mass, scissoring rate, length of the longest food item and feeding rate at natural nests) were log transformed to reduce positive skewness. Some nestlings scored zero for the number of food items ingested and scissoring rates, so we used the transformation $\log(x + c)$, where c is a constant which minimizes skewness by an iterative optimization process with 101 steps corresponding to increments in c within the range $0 < c < 20$. Predictor variables in linear models were centered to reduce collinearity and allow DF approximation for LMM (Quinn and Keough 2002, Singmann et al. 2015). Values given are means \pm SE.		
45	Data available from the Dryad Digital Repository: < http://dx.doi.org/10.5061/dryad.XXXXXX > (Romero and Redondo 2016).		[AQ1] 90
	Results		
50	Behaviour of parents and nestlings preceding food regurgitation		95
55	Typically, before a parent arrived with food, nestling storks remained being brooded or lying down, resting or making comfort movements (preening, stretching) in a non-ordered spatial distribution. As soon as a parent landed on the nest, chicks began to approach the parent while vocalizing, performing bill-clattering displays and waving their wings, until they placed themselves in a circle with their beaks converging to a point close to the adult’s feet. The time elapsed between arrival of the parent and food regurgitation was 98.5 ± 15.28 s ($n = 26$ nests). Latency to regurgitate food was independent from brood age and size (linear regression analysis with as independent variables brood age and brood size: $\beta = -0.49 \pm 2.29$, $t_{22} = 0.22$, $p = 0.83$, and $\beta = -11.75 \pm 16.55$, $t_{22} = 0.71$, $p = 0.48$, respectively). We could accurately measure times of nestlings approaching parents and subsequent food regurgitation at 18 different nests. Three broods younger than 8 days did not walk at all, but parents approached the group of chicks. The whole brood took an average of 56.7 ± 17.35 s ($n = 15$) to approach the adult until they stopped walking. Parents were never observed to disgorge food until all nestlings stopped walking and were together in a circle. At nests where nestlings took longer to form the circle, parents took more time to regurgitate food (Pearson’s $r = 0.57$, $p = 0.034$, $n = 14$). The average latency		100 105 110 115 121

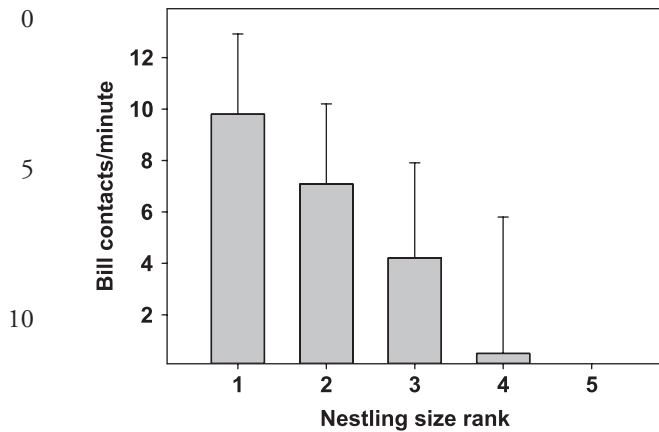


Figure 1. Pre-regurgitation scissoring rates of white stork nestlings according to mass rank within the brood (1 = heaviest). Error bars are standard errors around means.

for parents to regurgitate food after nestlings had formed the circle was 33.2 ± 9.87 s (range 0–122 s). Parents, therefore, fed chicks simultaneously in virtually all cases observed.

The time the adult bill was within a reaching distance sufficiently short for nestlings to perform scissoring behaviour was 48.2 ± 7.52 s ($n = 21$) and did not vary with either brood age or size (linear regression analysis with as independent variables brood age and brood size: $\beta = 51.14 \pm 857.63$, $t_{17} = 0.06$, $p = 0.95$, and $\beta = -1154.57 \pm 790.16$, $t_{17} = 1.46$, $p = 0.16$, respectively). At ten nests (32%), all containing nestlings younger than 13 d, parents never lowered their bill enough to be reached by nestlings before regurgitating food. Average scissoring rates for the whole brood neither varied with brood age nor brood size (linear regression analysis with as independent variables brood age and brood size: $\beta = 0.003 \pm 0.004$, $t_{17} = 0.84$, $p = 0.41$, and $\beta = 0.005 \pm 0.004$, $t_{17} = 1.28$, $p = 0.22$, respectively). Senior chicks scissored at higher rates than juniors (linear mixed-effects model LMM with nestling size rank as a fixed effect and nest as random: effect of rank $\beta = -0.38 \pm 0.07$, $F_{1,52.5} = 26.43$, $p < 0.001$). Actually, last-hatched nestlings in 4- and 5-chick broods were seldom able to contact the adult's bill (Fig. 1). In summary, senior chicks enjoyed a potential (but not realized) better chance to be fed first should parents have delivered food sequentially.

Food delivered at nests

Out of 35 feedings recovered by using nest collars at 30 different nests, only one (2.8%) consisted of a single food item. Seven feedings were composed exclusively by landfill

waste (mainly poultry and fish remains). Out of the 27 feedings containing natural prey, 9 (33.3%) were composed by the same food type and 18 (66.7%) by different types of prey. The most frequent prey types were earthworms (11 nests) and insects (11), followed by tadpoles (6), and crayfish (5) (Table 1). The average length of the largest food item was 61.2 ± 5.03 mm (range 20–150 mm).

Out of 40 natural feeding events recorded on video at 28 different nests, 2 (5%) consisted of a single food item and the remaining ones contained several food items (Table 1). Nine feedings consisted exclusively of landfill waste and the remaining ones contained the same prey as above, plus immature pond turtles (Table 1). Parents reingested food in 13 cases, all corresponding to broods younger than 17 d. Food reingested by parents consisted of items (pond turtles, crayfish and chicken debris) that nestlings had failed to swallow after several unsuccessful attempts. Summarizing, white stork parents in our study population fed nestlings with multiple prey items of varying size and difficulty to be handled by nestlings.

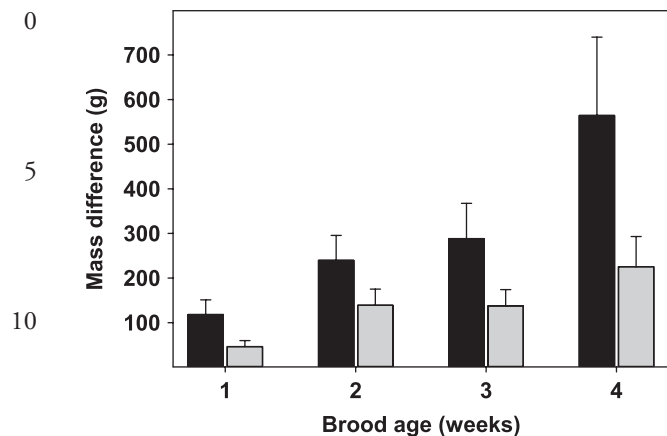
The size of the largest food item delivered by parents increased with the average mass of the brood (Linear regression analysis with as independent variable brood mass: $\beta = 0.28 \pm 0.09$, $t_{28} = 3.12$, $p = 0.004$) but this effect became non-significant when brood age and size were included in the model (linear regression analysis with as independent variables brood mass, age and brood size: average brood mass $\beta = 0.37 \pm 0.20$, $t_{26} = 1.80$, $p = 0.083$, brood age $\beta = -0.003 \pm 0.008$, $t_{26} = 0.43$, $p = 0.67$, and brood size $\beta = 0.015 \pm 0.032$, $t_{26} = 0.46$, $p = 0.65$). Neither the mass of the heaviest () nor the lightest chick in a brood explained a significant amount of variation in the length of the largest food item (linear mixed-effects model LMM with brood age, mass of the heaviest chick, and mass of the lightest chick as fixed effects and nest as random: heaviest chick mass $\chi^2 = 1.02$, $DF = 1$, $p = 0.31$, lightest chick mass $\chi^2 = 0.16$, $DF = 1$, $p = 0.68$). Most variation was explained by brood age ($\beta = 0.14 \pm 0.03$ SE, $\chi^2 = 7.87$, $DF = 1$, $p = 0.007$).

Food intake and handling speed according to nestling relative size

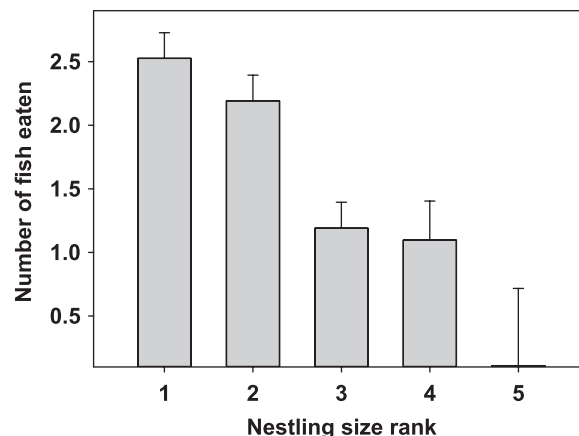
Differences in nestling mass due to asynchronous hatching were already evident during the first week of life, both for 3-chick (ANOVA, $F_{2,60} = 6.96$, $p = 0.002$, $n = 23$ broods, all years) and 4-chick broods (ANOVA, $F_{3,80} = 6.90$, $p < 0.001$, $n = 21$ broods, all years). Senior (heaviest) chicks not only maintained, but actually increased their size advantage relative to their younger nestmates throughout the first four weeks of life (Fig. 2). Mass differences between the

Table 1. Age variations across the first four weeks of life in the composition of food boluses regurgitated by stork parents, determined from samples collected using the neck-collar method ($n = 30$ broods) and from video recordings ($n = 29$).

Week	Length of the largest food item (mm)						Presence of prey categories (number of broods)				
	Mean	SE	n	Mean	SE	n	Earthworms	Insects	Tadpoles	Crayfish	Pond turtles
1	7.40	1.83	12	46.7	6.44	9	12	5	8	4	2
2	7.71	3.24	9	52.8	5.82	11	11	7	3	1	1
3	5.43	1.28	11	98.6	7.31	7	6	4	0	6	0
4	12.95	4.32	7	56.7	11.61	3	2	3	2	3	1



15 Figure 2. Weekly variations in mass differences of the heaviest nestlings in the brood with respect to their smallest broodmate (black bars) or the average mass of the remaining broodmates (grey bars). Error bars are standard errors around means.



61
65
70
75 Figure 3. The mean number of fish eaten (\pm SE) by nestlings according to their mass rank (1 = heaviest) during experimental feeding events.

20 heaviest and the lightest chicks in a brood increased with brood size (linear mixed-effects model LMM with brood size and age as fixed effects and nest as random: $\beta = 0.23 \pm 0.01$, $F_{1,42.28} = 13.26$, $p = 0.007$) and age ($\beta = 0.29 \pm 0.03$, $F_{1,18.7} = 61.36$, $p < 0.001$). Mass differences between the average nestling mass and the lightest chick in a brood followed a similar pattern (brood size $\beta = 0.23 \pm 0.06$, $F_{1,42.7} = 12.38$, $p = 0.001$, and age $\beta = 0.29 \pm 0.03$, $F_{1,18} = 58.27$, $p < 0.001$, respectively). Junior chicks, therefore, maintained their marginal condition all throughout the period of postnatal growth.

35 Experimental feeding tests revealed that nestlings preferred fish over prawns. Only 12 out of 87 (13.8%) nestlings picked up a prawn, compared to 86 nestlings (98.8%) picking up a fish. Out of the 12 nestlings that picked up prawns, only five at four different nests managed to swallow it (three were the largest chick in their brood and two the second-largest chick). Twelve nestlings that also picked up a fish also failed to swallow it and 10 of them were the smallest chicks in their brood.

40 Overall, during fish feeding tests, heavier nestlings ate a higher number of fish than smaller ones (Fig. 3). Nestling size rank had a negative effect upon fish handling time, i.e. heavier nestlings swallowed fish in a shorter time (linear mixed-effects model LMM with nestling size rank and brood size as fixed effects and chick nested within nest as random: effect of rank $\beta = -0.06 \pm 0.002$, $F_{1,59.6} = 5.68$, $p = 0.02$, effect of brood size $F_{1,19.5} = 0.71$, $p = 0.41$).

45 Chicks at natural nests completely consumed the food regurgitated by parents within a few minutes (mean 123.7 ± 16.80 s ($n = 31$ nests)). Feeding time did not vary with either brood age or size (linear regression analysis with as independent variables brood age and brood size: $\beta = 0.05 \pm 0.06$, $t_{28} = 0.86$, $p = 0.39$, and $\beta = 0.02 \pm 0.06$, $t_{28} = 0.27$, $p = 0.79$, respectively). Nestling size rank had a negative effect upon the rate of food intake (number of prey items swallowed): seniors ate more items than their junior nestmates (linear mixed-effects model LMM with nestling size rank, brood age and brood size as fixed effects and chick nested within nest as random: effect of rank $\beta = -0.07 \pm 0.02$,

80 $F_{1,64} = 9.88$, $p = 0.002$). The number of items ingested per chick did not vary with either brood age ($F_{1,78.6} = 0.21$, $p = 0.64$) or size ($F_{1,70.5} = 0.10$, $p = 0.75$). Larger nestlings typically consumed larger food items than smaller ones but this was not adequately quantified. The total number of food items ingested by the whole brood neither varied with brood age or size (linear regression analysis with as independent variables brood age and brood size: $\beta = 0.0005 \pm 0.0084$, $t_{28} = 0.06$, $p = 0.95$, and $\beta = 0.03 \pm 0.06$, $t_{28} = 0.57$, $p = 0.57$, respectively).

Competition by direct physical interference during feeding events

95 Parental regurgitations comprised a single food bolus in 39 out of 44 cases. In 5 different broods younger than 8 d, parents fractioned the food in 2–4 boluses delivered in a single bout. Virtually all food boluses were indirect, i.e. nestlings picked up all the food from the nest floor before swallowing it. In 31 out of 41 filmed feeding events (75.6%) all nestlings in the brood ingested some food. In nine cases, one chick in each brood failed to eat any food: the youngest one (5 cases, 11.9%), the largest one (2 cases) and the second largest one (2 cases). At one feeding event, none of the chicks managed to eat any food at all. The oldest nestling in five different broods older than 20 d (containing 2 or 3 chicks) inserted its bill into the adult's and grasped it firmly while scissoring, but in all cases the adult pulled it away from the nestling before regurgitating food.

100
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121 Nestlings, even very young ones, waved their wings half-spread while eating food in all the observed feeding events. Only 3 nestlings (1.3% of all feeding events) at two different nests 3 and 4 weeks old containing 2 and 3 chicks completely spread their wings while feeding, but this did not cause their adjacent nestmates to be displaced from the food source. Typically, nestlings spread their wings over the back of their nestmates. We never observed chicks obstructing or pushing siblings aside while food was present. Nestlings remained stationary in the circle for as long as food was present, only

0 performing minor balancing movements while swallowing
 food or bill-clattering.

We observed aggressions (pecks) in 7 feeding episodes at
 7 different nests three and four weeks old (5 and 2 nests,
 respectively). These broods contained between 2 and 4
 chicks. All aggressions were directed at incoming adults when
 attempting to land on the nest and involved all nestlings
 in the brood except the youngest ones. No other form of
 aggression was observed, neither threat displays among
 nestlings.

10 **Food disputes**

We observed 19 cases (at 15 different nests) where nestlings
 got involved in a non-aggressive food dispute out of 41 natural
 feeding events (32 different nests). 11 such cases involved
 tugs-of-war (two nestlings grasping and pulling from the
 same food item at the same time) and 16 involved a nest-
 ling assaulting a nestmate which was attempting to swallow
 a large food item (7 events involved both). During experi-
 mental feeding tests, we observed 18 food disputes out of
 29 feeding events at 25 different nests (11 tugs-of-war and
 9 assaults, 2 both). The fraction of nests at which disputes
 occurred was similar for natural (15/32) and experimental
 (18/29) feeding events (Fisher's exact $p = 0.306$). At natural
 nests, the frequency of disputed feeding events was minimal
 during the first week after hatching (3/12, 25%) and peaked
 on the third week (10/15, 67%). Chicks acting as recipients
 of a food assault made no attempt to avoid being robbed,
 apart from pulling and attempting to swallow the food item.
 They did not leave the feeding circle attempting to hide or
 conceal the food.

We hypothesized that food disputes were a competitive
 mechanism by which heavier chicks obtained a larger
 food share at the expense of their younger nestmates. This
 hypothesis generated several predictions that we tested using
 data from both natural and experimental feeding events. The
 predictions were as follow.

1) Food disputes should be more frequent in larger broods
 This prediction was not supported. The probability that a
 feeding event involved a food dispute did not show any clear
 pattern according to brood size (Table 2).

2) Junior nestlings should be most involved in food
 disputes as victims. The most frequent chick dyads for both
 tugs-of-war (Table 3) and assaults (Table 4) involved the
 two oldest senior nestlings in a brood, rather than a senior
 and a junior. In 5-chick broods, the youngest nestling was

Table 3. Composition of dyads according to nestling size rank in
 tug-of-war interactions and the percentage of nestlings of a given
 size rank that were involved.

	Nestling size rank			% Nestlings involved	n
	1	2	3		
Nestling size rank					
1	–			100.0	20
2	13	–		70.0	20
3	5	0	–	29.4	17
4	2	1	0	37.5	8

never observed to be involved in a food dispute. In 18 out of
 20 (90%) tugs-of-war at different nests, the winner was the
 largest chick (Binomial test, $p < 0.001$). Nestlings acting as
 actors in an assault won the dispute in 15 out of 23 (65.2%)
 cases at different nests (Binomial test, $p = 0.210$). The
 heaviest chick in a dyad won 69.5% of assaults (Binomial
 test, $p = 0.094$), independently of its role as actor or receiver.
 In summary, while the heaviest chick in a dyad won most of
 the food disputes, these did not involve the smaller chicks
 in a brood.

3) Chicks winning a dispute should eat more food.
 Data from experimental feeding tests, where food items
 were of the same size, showed that chicks winning a tug-
 of-war ate a similar number of fish (2.36 ± 1.12 fish) than
 loser chicks (2.64 ± 0.81 fish) (paired t test, $t_{10} = 0.61$,
 $p = 0.85$, $n = 11$ dyads). Chicks winning an assault ate on
 average 2.30 ± 1.34 while those losing it ate 1.2 ± 1.02 fish
 (paired t test, $t_9 = 1.77$, $p = 0.12$, $n = 10$ dyads at 9 nests).
 Overall, nestlings winning a dispute ate a similar number of
 fish (2.40 ± 0.26) than their loser nestmates (1.95 ± 0.27),
 but statistical power was too low ($t_{20} = 1.21$, $p = 0.31$,
 $PW = 0.17$) to allow drawing any conclusion from this
 comparison.

Discussion

This is the first detailed study aimed at quantifying the
 frequency and intensity of behavioural mechanisms of nest-
 mate competition during the critical phase of postnatal
 growth in a species of stork. As a general result, it validates
 previous verbal statements (Tortosa and Redondo 1992,
 Klosowski et al. 2002, Zielinski 2002, Djerdali et al. 2008a)
 that competition among white stork nestlings follows a
 scramble distribution of resources mediated by differences
 in the velocity of food eating by nestlings according to
 their size, rather than a despotic sharing caused by phys-
 ical interference or aggression. Heavier chicks were more
 efficient handling food items and ate more food at both
 experimental and natural feeding events. After careful
 screening for a wide repertoire of behavioural mechanisms
 (aggression, monopolization, dominance, blocking, sup-
 planting and robbing food from unwilling junior nestmates)
 which are often observed in similar bird species, we found
 little evidence of direct physical interference among white
 stork broodmates. Despite considerable asymmetries in size
 and potential to exert physical power, seniors were tolerant
 by allowing juniors to eat as much food as they could (by
 virtue of their eating speed) without attacking, obstructing,

Table 2. The fraction of natural and experimental feeding events in
 which food disputes were observed as a function of brood size.

	Brood size			
	2	3	4	5
Natural				
Disputed	5	8	6	1
n	12	16	15	4
% Disputed	41.7	50.0	40.0	33.3
Experimental				
Disputed	1	8	7	2
n	2	13	11	3
% Disputed	50.0	61.5	63.6	66.7

0 Table 4. Composition of dyads in assault interactions according to nestling size rank and role (actor vs receiver) and the percentage of nestlings of a given rank that were involved in any role. 61

		Actor size rank				% As actor	% As receiver	n
		1	2	3	4			
5	Receiver size rank							65
	1	–	4	0	0	77.3	18.2	22
	2	12	–	1	0	18.2	59.0	22
	3	3	0	–	0	10.0	15.0	20
	4	2	0	1	–	0.0	42.8	7

10 supplanting or otherwise interfering with them. This tolerance can be regarded as a simple form of prosocial behaviour because it benefits junior nestmates by reducing distress or need (Roulin et al. 2016). We never observed nestlings behaving altruistically towards siblings (e.g. by actively feeding them, as in barn owls, Roulin et al. 2012) but it may be asked whether seniors would have grown better by limiting or suppressing feeding by juniors. According to Sasvári et al. (1999a), seniors in nests where some broodmates had died attained larger asymptotic masses. This general result can be considered representative of other white stork populations on the basis of similarities in patterns of asynchronous hatching and size asymmetries (Tortosa 1992, Aguirre and Vergara 2007, Djerdali et al. 2008a), nestling diet (Tsachalidis and Goutner 2002, Kosicki et al. 2006, Cheriak et al. 2014), rates of parental provisioning (Schüz 1943, Haverschmidt 1949, Sasvári et al. 1999b), postnatal growth (Tortosa and Castro 2003, Tsachalidis et al. 2005, Benharzallah et al. 2015) and food distribution according to nestling rank (Sasvári et al. 1999a). Broodmate competition is dependent on food availability to some degree (Drummond 2001b). Hence, the possibility remains that our results may not be applicable for other white stork populations in case our study region represents a prime habitat with exceptionally abundant food. This is unlikely, however, because breeding performance in our study population was not particularly good. Food availability is known to increase clutch and brood size (both at hatching and fledging time) in white storks (Denac 2006, Massemin-Challet et al. 2006, Djerdali et al. 2008b). In our study population during 2002–2003, average clutch size was 3.9 (± 0.11 SE, $n = 56$) eggs, brood size at hatching was 3.2 (± 0.08 SE, $n = 49$) chicks and brood size at 40–45 d was 2.31 (± 0.09 SE, $n = 107$). These values are similar to other populations (Cramp and Simmons 1977) and indeed are lower than those recorded by Sasvári et al. (1999b) (3.87–4.51 eggs, 3.46–4.22 hatchlings, and 2.49–3.90 fledglings) in their study population, where intra-brood competition was presumably intense (Sasvári et al. 1999a).

50 Aggression in nestling storks

Despite obvious asymmetries in resource holding potential due to differences in nestling mass within broods, we failed to find any evidence of aggressive sibling rivalry. Nestlings in this study (particularly seniors) were capable of aggressive attacks after their second week of age but aggressions were directed at incoming parents (already described by Cramp and Simmons 1977). No aggression between nestlings was ever observed, neither threat of submissive displays indicative of an aggressive dominance hierarchy (Drummond 2006). A

characteristic absence of agonistic interactions among white stork nestlings has been previously reported by other authors (Schüz 1943, Haverschmidt 1949, Tortosa and Redondo 1992). Cramp and Simmons (1977, p. 334) wrote that ‘Siblings do not fight among themselves (F. Haverschmidt) unless hungry, when disputes often intense and lead to death through starvation of smallest (M. P. Kahl)’. However, no study has ever reported sibling aggression below 20 d of age, when 91% of nestling mortality occurs (Jovani and Tella 2004). Actually, Kahl (1972b, p. 245) did not mention aggression or even physical interference at all but stated that ‘Competition between nestlings for food is often intense, and, in a nest with several young, the largest is at a great advantage, owing to its greater strength and speed’. However, two more detailed studies reported aggressive interactions at the end of the nestling period. Redondo et al. (1995) observed frequent fights among siblings at these ages but they concluded that most of them were the result of a defensive response against kleptoparasitic alien chicks that failed, however, to discriminate between resident and foreign chicks. Sasvári et al. (1999a) reported senior chicks pecking at younger siblings when 60–65 d old, but not during the first two weeks of life, when nestling mortality occurred. According to its function of biasing parental resources and maintaining dominance to ensure biased investment in the future in other species (Drummond 2001a), aggression is expected to be more prevalent in the initial phases of the nestling period (Mock and Lamey 1991, Drummond 2001a, 2006, Gonzalez-Voyer and Drummond 2007). Chick fighting between 8-weeks old white stork nestlings clearly does not fit into this pattern because nestlings have already completed growth two or three weeks before (Tortosa and Castro 2003, Tsachalidis et al. 2005) and will soon become nutritionally independent from parents at 75–90 d of age (Haverschmidt 1949, Redondo et al. 1995, Corbel and Groscolas 2008). We know of no other published study reporting sibling aggression in other ciconiid species, but several authors explicitly mention the lack of it (maguari stork *Ciconia maguari* Thomas 1984, black stork Klosowski et al. 2002). However, Urfi (2011) described threat displays (but not aggression) among half-grown nestlings of the painted stork.

Non-aggressive interference competition in nestling storks

We found little, if any, evidence of physical interference among white stork nestlings in this study. Senior chicks were never observed to trample, push, supplant or prevent in any form their junior nestmates from reaching the clump of food,

0 despite it was concentrated at a precise location in the nest. When explaining how some last-hatched stork nestlings suffered from retarded growth and became runts, Haverschmidt (1949, p. 51) wrote that 'it is *obvious* that these smaller and weaker young are pushed aside by the older and stronger nestlings' (our emphasis), but he apparently assumed that such behaviour was likely to occur, rather than actually observed it. Physical interference has been reported in only two stork species. Pushing and jostling has been observed in jabiru stork nestlings (J. Villarreal-Orias pers. comm.). In the African openbill stork, nestlings prevent others from eating food by opening their wings (Kahl 1972a). In the same line as above, we never observed nestlings to physically interfere with each other by attempting to gain a favourable position close to the adult's bill in order to obtain direct feedings. The question of whether white stork nestlings compete for direct feedings is a somewhat controversial topic. For example, Brown et al. (1982, p. 184), quoting Cramp and Simmons (1977), state that chicks older than 12 d '...can feed directly from the adult's bill'. The original source describing this transition in nestling behaviour can be traced back to Schüz (1943), later quoted by Haverschmidt (1949, p. 45): 'When growing older, however, according to Schüz (1943) from 12 d onwards, they *try* to get hold of the old bird's bill' (our emphasis). By contrast, Sasvári et al. (1999a, p. 572) monitored 14 nests 5–15 d old with the aid of binoculars and 'recorded which chicks were the first to receive food on the arrival of the parent'. They found that senior chicks were more likely to be fed first, particularly in nests where one or two chicks had previously died. This result is particularly puzzling, not only because it is the only case of direct feeding of white stork nestlings at such young ages (cf. Schüz 1943), but also because it is unique in reporting sequential chick feeding by white stork parents. All other studies of parental feeding behaviour in white storks describe parents feeding young not in a sequential manner, but simultaneously when nestlings are sitting in a circle (Schüz 1943, Haverschmidt 1949, Kahl 1972b, Hancock et al. 1992, also Sasvári and Hegyi (2001) for chicks older than 20 d). One possible explanation is that Sasvári et al. (1999a) inferred (erroneously) direct food transfer from observing scissoring rates. In this study, we found that senior nestlings had higher scissoring rates and probably were more rapid in contacting the adult's bill but this was due in part to their larger size (height), not because they were fed first by parents (see Ploger and Mock (1986) and Parker et al. (1989) for similar results in egrets). Nevertheless, the possibility remains that different populations may vary in the proportion of feedings directly taken from the parent's bill, perhaps depending on the amount of food received (Creighton and Schnell 1996).

10 The only evidence suggestive of interference competition found in this study comes from dyadic competitive interactions for the same food item, in the sense that heavier nestlings were more likely to end winning the food dispute. However, food disputes were not more frequent in larger broods (where the amount of food per capita is presumably lower (Sasvári et al. 1999a, b), and seldom involved the youngest chicks. Junior chicks might refrain from entering a food contest given their inferior competitive abilities, but it is unclear how they could avoid participating as unwitting victims. Junior chicks are the most frequent victims of intimidations and food losses in species showing overt sibling rivalry (Ploger and Mock 1986, Mock and Parker 1997). Most remarkably, chicks that were assaulted by a nestmate while attempting to eat a large food item made no visible attempt to avoid being robbed, apart from pulling and attempting to swallow the disputed food item. By contrast, in species (e.g. barn owls) where nestlings compete by food thieving, assaulted chicks attempted to contest, hide or conceal food from stealers (Roulin et al. 2008). This provides weak support to the hypothesis that food disputes were a behavioural mechanism of interference competition by which senior nestlings used their superior physical powers to steal food from younger chicks. An alternative explanation is that food disputes merely arose as a result of senior siblings attempting to swallow large food items before the adults reingested them. Adult storks often reingest some of the food items they have just regurgitated onto the nest, particularly during the first weeks after hatching (Schüz 1943, Haverschmidt 1949). Consistent with this interpretation, disputed food items at natural nests were usually of a large size and mainly involved the two heaviest chicks because younger nestlings seldom attempted to eat food items that were difficult to handle (e.g. prawns in experimental feeding tests). In this sense, the higher probability of heavier nestlings winning a dispute may be a passive result of their superior strength, much in the same way as they were able to handle prey more efficiently than younger ones.

Summarizing, white stork nestlings competed for food by purely scramble mechanisms (eating speed) and virtually lacked behavioural mechanisms (aggressive dominance or physical interference) of interference competition. In the absence of food monopolization by seniors, scramble competition may be a sufficient explanation for differential patterns of growth (Benharzallah et al. 2015) and share of food mass (Sasvári et al. 1999a) according to nestling rank. Consistent with this scenario of mild sibling rivalry, and contrary to species showing overt interference or aggressive competition, white stork nestlings showed no differences in glucocorticoid levels associated with brood hierarchy, and stress hormone levels were similar among two- and three-chick broods (Blas et al. 2005, Corbel and Groscolas 2008). This pattern of high tolerance by senior nestlings is shared by most stork species but it is exceptional (Zielinski 2002) among other bird families with many ecological and phylogenetic affinities, in particular egrets and herons.

What makes storks special for senior nestlings being tolerant?

Both aggression and overt physical interference are probably costly to nestlings in terms of energy, time and risk (Ploger and Mock 1986, Mock and Lamey 1991, Drummond 2002). One possible explanation for reduced interference competition in white stork chicks is that the cost of falling out of the nest (Bize and Roulin 2006) is higher in storks than in other birds like herons or ibises. The latter species often breed in tree bushes where chicks could climb back to the nest. Storks build more isolated nests where any chick that falls out of the nest will not be able to climb back. Falling out of the nest accounted for 12% (4/33) white stork chick losses and only affected nestlings 4–5 weeks old

[AQ3] 0 (Tortosa 1992). Stork chicks older than 45 d are able to fly short distances (Redondo et al. 2005) and this could explain why aggression is only observed at the end (60–70 d) of the nestling period, when nestlings do not risk falling out of the nest. The main problem with this hypothesis is that, by that age, chicks have already completed growth and plumage development and are about to become nutritionally independent from parents. Therefore, costs of broodmate aggression at the end of the period of parental care may be negligible, but its potential benefits are equally so. Falling out of the nest is a major cause of mortality in egrets and herons too (Mock and Parker 1986, 1997, Si Bachir et al. 2008). Actually, in at least 27% of siblicidal events among great egret broods, victimized chicks did not die from injuries or starvation at their nest, but were driven away by seniors (Mock 1985).

15 Most avian species showing nestmate aggression (as well as interference competition) are, like storks, semialtricial carnivorous birds which typically show slow rates of food transfer (compared, for example, with passerines) from parents to offspring (Mock and Parker 1997, Drummond 2002, 2006). Within these bird groups, sibling aggression (or competitive interference) may be less effective in species with: 1) larger broods (Drummond 2001a, 2002, Gonzalez-Voyer et al. 2007), 2) long nestling periods (Gonzalez-Voyer et al. 2007), and 3) large asymmetries in nestling age and size (Mock and Parker 1997). However, none of these traits can satisfactorily explain the low level of competitive interference typical of stork broods. For example, at least 8 species of herons showing intense or occasional sibling aggression also lay 4-egg modal clutches at 2 d intervals, commence incubation with the first egg, and have indeed shorter nestling periods than white storks (Meanley 1955, Inoue 1985, Mock 1985, 1987, Marchant and Higgins 1990, Holmes and Hatchwell 1991, Lekuona and Campos 1998, Medeiros et al. 2000, Kushlan and Hancock 2005).

30 Mild or absent sibling rivalry among stork nestlings has been traditionally explained in terms of parents discouraging sibling competition by feeding nestlings simultaneously (thus, indirectly) with multiple, non-monopolizable food items (Thomas 1984, Tortosa and Redondo 1992, Klosowski et al. 2002, Zielinski 2002, Djerdali et al. 2008a). Adults in other bird species have been shown to reduce the intensity of scramble competition among nestlings by implementing egalitarian feeding tactics (Blanc et al. 2010, Du et al. 2012). Parents in this study seemed to favour younger nestlings by 1) not disgorging food until all nestlings were placed together in a circle, 2) pulling away their bill from senior nestlings that attempted to obtain direct feedings, and 3) provisioning nestlings with multiple food items of variable size and handling difficulty. In an experimental study where the mass of the heaviest chick was artificially doubled, white stork parents responded by delivering larger prey but also increased the total food amount so that smaller chicks were not disadvantaged (Djerdali et al. 2008a).

45 It is not entirely clear in the above explanation whether interference competition among stork nestlings is discouraged by either indirect feeding or lack of monopolizable food items (Tortosa and Redondo 1992, Zielinski 2002). The feeding method ('prey size' Mock 1985, Mock and Parker 1997) hypothesis holds that aggression (but also competitive interference) should be less effective when food is deposited on the nest floor. This hypothesis however has not received empirical support (Drummond 2001a, 2002, Gonzalez-Voyer and Drummond 2007) and comparative data actually suggest more frequent aggressive exclusion of broodmates from food dumped on the nest (Gonzalez-Voyer et al. 2007). The food parcel hypothesis states that when parents transfer food in large and infrequent parcels fractioned (clustered) in bouts or meals, each parcel becomes economically defensible, and it pays nestlings to implement costly competitive mechanisms such as aggression, independently of the feeding method (Drummond 2002, Gonzalez-Voyer et al. 2007). Unlike storks, herons usually deliver the food fragmented into series of small boluses that can be monopolized by nestlings (Ploger and Medeiros 2004). Fragmented food is common even in heron species whose nestlings feed mainly from food regurgitated on the nest floor (Werschkul 1979, Fujioka 1985, Marchant 1988, Marchant and Higgins 1990, Hafner et al. 1993, Medeiros et al. 2000, McRimmon et al. 2011). By contrast, storks only seldom fractionate the food bolus, regurgitating a large amount of food onto the nest that can be accessed by several nestlings simultaneously (Hoogerwerf 1936, Haverschmidt 1949, Kahl 1966, 1971a, b, 1972a, b, c, Thomas 1984, Hancock et al. 1992, Danielsen et al. 1997, Coulter et al. 1999, Klosowski et al. 2002, Maheswaran and Rahmani 2005, Falk et al. 2006, Urfi 2011; but see Thomas (1984) and Coulter et al. (1999) for adults fractioning the food bolus when caring for very young nestlings).

85 By varying the degree of food fragmentation, parents may exert some control upon the ability of senior nestlings to monopolize food (Mock and Parker 1997, Drummond 2002, Shen et al. 2010). However, once food has been deposited on the nest, senior nestlings could still prevent their junior nestmates from eating food by attacking or pushing them aside until they are satiated, as in aggressive northern goshawk *Accipiter gentilis* (Byholm et al. 2011) and yellow-crowned night herons *Nyctanassa violacea*, where nestlings were observed to trample, push and peck at their siblings while feeding simultaneously from food dumped on the nest (Bagley and Grau 1980). In other words, parental enforcement may facilitate, but fails to adequately explain tolerance by senior nestlings (Drummond 2006).

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