Kind to kin: weak interference competition among white stork *Ciconia ciconia* broodmates

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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).

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).

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).

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

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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).

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 analysis 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, Threskiornithidae), 54% (egrets and herons, Ardeidae), 69% (accipiters Accipitridae), and above 90% 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).

Storks (Ciconiidae) share many ecological and phylogenetic 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 interference 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 family life. In at least two species (the white and black stork *Ciconia nigra*), parents are known to sometimes practice filial infanticide, directly killing their smallest offspring (Schüz 1943, Haverschmidt 1949, Tortosa and Redondo 1992, Klosowski et al. 2002, Zielinski 2002). Confirmed cases of 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 behaviour 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. 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 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 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 et al. 2002). Other possible mechanisms of non-aggressive interference competition (e.g. food thieving, obstructing or suplanting 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 (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 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 afterwards. White stork parents make optimistic decisions by 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 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 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 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. 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 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 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

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 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).

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 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 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 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 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 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 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.

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, 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.

Methods

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.

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.

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.

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

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.

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 2.5 m long, which was fastened to tree branches by several 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 placing 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 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 feeding events per nest at the most. Out of 444 h of video, we 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 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.

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 nests are remarkably large (80–150 cm diameter on average, 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 to feeding was measured as the time since the first nestling 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 measured occurrences of some specific behaviours potentially 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, 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 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 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 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 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 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 *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 nestlings 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' 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 by two nestlings simultaneously. Food disputes might give heavier chicks a competitive advantage, as in hen harriers *Cyrcus 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* 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 swallowing the food item and to lose it if the food was eaten by its opponent. In the case of food assaults, we also recorded 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 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 nests (for the validity of this method see Hampl et al. 2005

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

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 *Procambarus clarkii*. 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.

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 (*Engraulis* sp.) and prawns (*Parapenaeus* 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.

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).

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. Nests were revisited at 45–50 d to ring nestlings.

Statistical analyses

Statistical analyses were performed in R (R Core Team). To account for lack of statistical independence (Hurlbert 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.

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.XXXXX> (Romero and Redondo 2016).

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Results

Behaviour of parents and nestlings preceding food regurgitation

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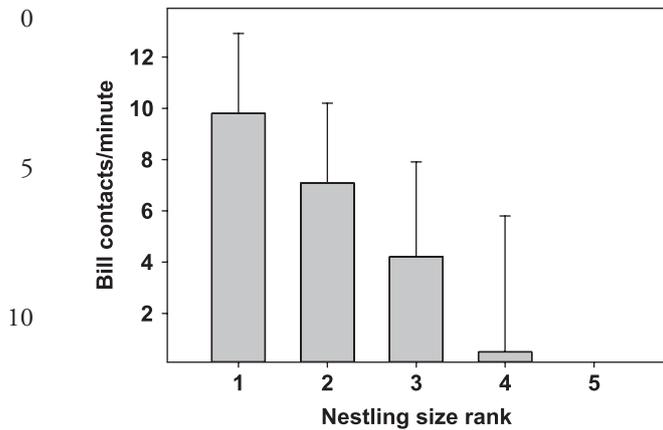
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Figure 1. Pre-regurgitation scissoring rates of white stork nestlings according to mass rank within the brood (1 = heaviest). Error bars are standard errors around means.

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).

	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
Week											
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

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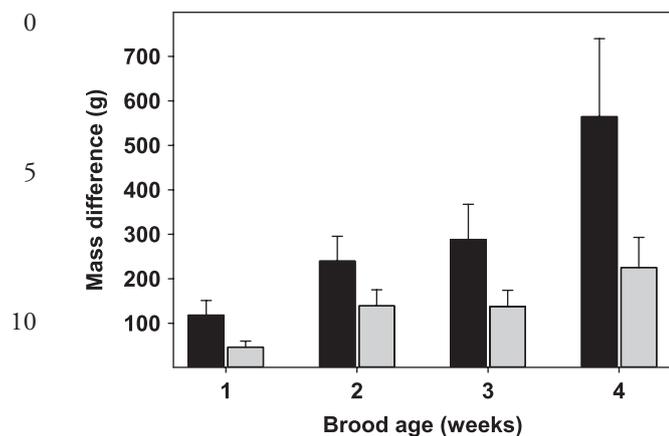
Figure 2. Weakly variations in mass differences of the heaviest nestlings in the brood with respect to their smallest broodmate (black bars) or the average mass of the remaining broodmates (grey bars). Error bars are standard errors around means.
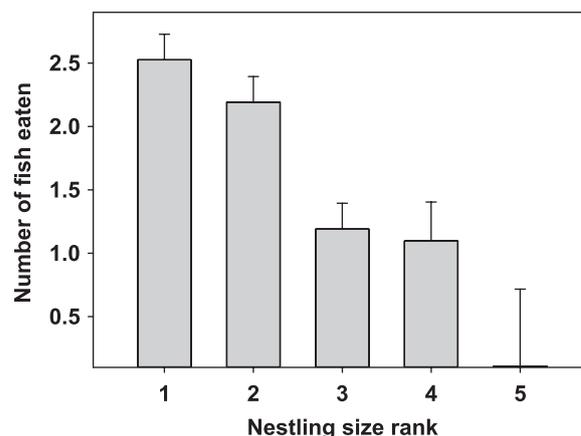
heaviest and the lightest chicks in a brood increased with brood size (linear mixed-effects model LMM with brood size and age as fixed effects and nest as random: $\beta = 0.23 \pm 0.01$, $F_{1,42.28} = 13.26$, $p = 0.007$) and age ($\beta = 0.29 \pm 0.03$, $F_{1,18.7} = 61.36$, $p < 0.001$). Mass differences 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 througout the period of postnatal growth.

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.

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 $F_{1,19.5} = 0.71$, $p = 0.41$).

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 $\beta = -0.07 \pm 0.02$,

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

$F_{1,64} = 9.88$, $p = 0.002$). 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

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.

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

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.

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 nestling assaulting a nestmate which was attempting to swallow a large food item (7 events involved both). During experimental 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 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

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				
	1	2	3	% Nestlings involved	n
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 physical 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, supplanting and robbing food from unwilling junior nestlings) 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,

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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.

	Actor size rank				% As actor	% As receiver	n
	1	2	3	4			
Receiver size rank							
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

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 ($\pm$ 0.11 SE, n = 56) eggs, brood size at hatching was 3.2 ($\pm$ 0.08 SE, n = 49) chicks and brood size at 40–45 d was 2.31 ($\pm$ 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).

Aggression in nestling storks

Despite obvious asymmetries in resource holding potential due to differences in nestling mass within broods, we failed to found 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,

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).

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

(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).

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).

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).

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 defendable, 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).

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).

References

Aguirre, J. I. and Vergara, P. 2007. Younger, weaker white stork (*Ciconia ciconia*) nestlings become the best breeders. – Evol. Ecol. Res. 9: 355–364.

Bagley, F. M. and Grau, G. A. 1980. Aspects of yellow-crowned night heron reproductive behavior. – Colon. Waterbirds 3: 165–175.

Balfour, E. and Macdonald, M. A. 1970. Food and feeding behaviour of the hen harrier in Orkney. – Scot. Birds 6: 57–66.

Bates, D., Maechler, M., Bolker, B. and Walker, S. 2014. lme4: linear mixed-effects models using Eigen and S4. – R package ver. 1.1-7, <http://CRAN.R-project.org/package=lme4>.

Benharzallah, N., Bachir, A. S., Taleb, F. and Barbraud, C. 2015. Factors affecting growth parameters of white stork nestlings in eastern Algeria. – J. Ornithol. 156: 601–612.

Bize, P. and Roulin, A. 2006. Sibling competition and the risk of falling out of the nest. – Anim. Behav. 72: 539–544.

Blanc, A., Ogier, N., Roux, A., Denizeau, S. and Mathevon, N. 2010. Begging coordination between siblings in black-headed gulls. – C. R. Soc. Biol. 333: 688–693.

Blas, J., Baos, R., Bortolotti, G. R., Marchant, T. and Hiraldo, F. 2005. A multi-tier approach to identifying environmental stress in altricial nestling birds. – Funct. Ecol. 19: 315–322.

Braun, B. M. and Hunt, G. L. 1983. Brood reduction in black-legged kittiwakes. – Auk 100: 469–476.

Byholm, P., Rousi, H. and Sole, I. 2011. Parental care in nesting hawks: breeding experience and food availability influence the outcome. – Behav. Ecol. 22: 609–615.

Cheriak, L., Barbraud, C., Doumandji, S. and Bouguessa, S. 2014. Diet variability in the white stork *Ciconia ciconia* in eastern Algeria. – Ostrich 85: 201–204.

Corbel, H. and Groscolas, R. 2008. A role for corticosterone and food restriction in the fledging of nestling white storks. – Hormon. Behav. 53: 557–566.

Cotton, P. A., Wright, J. and Kacelnik, A. 1999. Chick begging strategies in relation to brood hierarchies and hatching asynchrony. – Am. Nat. 153: 412–420.

Coulter, M. C., Rodgers, J. A., Ogden, J. C. and Depkin, F. C. 1999. Wood stork (*Mycteria americana*). – In: Poole, A. (ed.), The birds of North America online. Cornell Lab of Ornithology, <http://bna.birds.cornell.edu/bna/species/409>.

Cramp, S. and Simmons, K. E. L. 1977. Handbook of the birds of Europe, the Middle East and North Africa. The birds of Western Paleartic. Vol. 1 and 2. – Oxford Univ. Press.

Creighton, J. C. and Schnell, G. D. 1996. Proximate control of siblicide in cattle egrets: a test of the food-amount hypothesis. – Behav. Ecol. Sociobiol. 38: 371–377.

Danielsen, F., Kadarisman, R., Skov, H., Suwarman, U. and Verheugt, W. J. 1997. The Storm's stork *Ciconia stormi* in Indonesia: breeding biology, population and conservation. – Ibis 139: 67–75.

Denac, D. 2006. Resource-dependent weather effect in the reproduction of the white stork *Ciconia ciconia*. – Ardea 94: 233–240.

Djerdali, S., Tortosa, F. S. and Doumandji, S. 2008a. Do white stork (*Ciconia ciconia*) parents exert control over food distribution when feeding is indirect? – Ethol. Ecol. Evol. 20: 361–374.

Djerdali, S., Tortosa, F. S., Hillstrom, L. and Doumandji, S. 2008b. Food supply and external cues limit the clutch size and hatchability in the white stork *Ciconia ciconia*. – Acta Ornithol. 43: 145–150.

Dolata, P. T. 2006. "Close to storks" – a project of on-line monitoring of the white stork *Ciconia ciconia* nest and potential use of on-line monitoring in education and research. – In: Tryjanowski, P., Sparks, T. H. and Jerzak, L. (eds), The white stork in Poland: studies in biology, ecology and conservation. Bogucki Wyd. Nauk., pp. 437–448.

Dreiss, A. N., Gaime, F., Delarbre, A., Moroni, L., Lenarth, M. and Roulin, A. 2016. Vocal communication regulates sibling competition over food stock. – Behav. Ecol. Sociobiol. 70: 927–937.

Drummond, H. 2001a. The control and function of agonism in avian broodmates. – Adv. Stud. Behav. 30: 261–301.

Drummond, H. 2001b. A reevaluation of the role of food in broodmate aggression. – Anim. Behav. 61: 517–526.

Drummond, H. 2002. Begging versus aggression in avian broodmate competition. – In: Wright, J. and Leonard, M. L. (eds), The evolution of begging: competition, cooperation and communication. Kluwer Academic Publishers, pp. 337–360.

Drummond, H. 2006. Dominance in vertebrate broods and litters. – Q. Rev. Biol. 81: 3–32.

Du, B., Zhao, Q. S., Liu, C. J., Guan, M. M. and Liu, N. F. 2012. Giant babaxes mix brood reduction and brood survival strategies. – J. Ornithol. 153: 611–619.

Falk, K., Jensen, F. P., Christensen, K. D. and Petersen, B. S. 2006. The diet of nestling Abdim's stork *Ciconia abdimii* in Niger. – Waterbirds 29: 215–220.

Forbes, L. S. 1993. Avian brood reduction and parent–offspring "conflict". – Am. Nat. 142: 82–117.

Forbes, S. 2007a. A natural history of families. – Princeton Univ. Press.

Forbes, S. 2007b. Sibling symbiosis in nestling birds. – Auk 124: 1–10.

Forbes, S. 2010. Family structure and variation in reproductive success in blackbirds. – Behav. Ecol. Sociobiol. 64: 475–483.

Forbes, S. 2011. Social rank governs the effective environment of siblings. – Biol. Lett. 7: 346–348.

Fujioka, M. 1985. Sibling competition and siblicide in asynchronously-hatching broods of the cattle egret *Bubulcus ibis*. – Anim. Behav. 33: 1228–1242.

Gonzalez-Voyer, A. and Drummond, H. 2007. Is broodmate aggression really associated with direct feeding? – Behaviour 144: 373–392.

Gonzalez-Voyer, A., Székely, T. and Drummond, H. 2007. Why do some siblings attack each other? Comparative analysis of aggression in avian broods. – Evolution 61: 1946–1955.

Hafner, H., Dugan, P. J., Kersten, M., Pineau, O. and Wallace, J. P. 1993. Flock feeding and food intake in little egrets *Egretta garzetta* and their effects on food provisioning and reproductive success. – Ibis 135: 25–32.

Hampl, R., Bureš, S., Baláž, P., Bobek, M. and Pojer, F. 2005. Food provisioning and nestling diet of the black stork in the Czech Republic. – Waterbirds 28: 35–40.

Hancock, J. A., Kushlan, J. A. and Kahl, M. P. 1992. Storks, ibises, and spoonbills of the world. – Academic Press.

Haverschmidt, F. 1949. The life of the white stork. – E. J. Brill.

Herring, G., Gawlik, D. E., Cook, M. I. and Beerens, J. M. 2010. Sensitivity of nesting great egrets (*Ardea alba*) and white ibises (*Eudocimus albus*) to reduced prey availability. – Auk 127: 660–670.

Holmes, P. R. and Hatchwell, B. J. 1991. Notes on the ecology of the little bittern *Ixobrychus minutus* at Haigam Rakh, Kashmir, India. – Forktail 6: 25–33.

Hoogerwerf, A. 1936. Met de camera naar de Nimmerzatten. – Tropische Nat. 25: 83–96.

Hudson, R. and Trillmich, F. 2008. Sibling competition and cooperation in mammals: challenges, developments and prospects. – Behav. Ecol. Sociobiol. 62: 299–307.

Hunt, J. D. and Evans, R. M. 1997. Brood reduction and the insurance-egg hypothesis in double-crested cormorants. – Colon. Waterbirds 20: 485–491.

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. – Ecol. Monogr. 54: 187–211.

Inoue, Y. 1985. The process of asynchronous hatching and sibling competition in the little egret *Egretta garzetta*. – Colon. Waterbirds 8: 1–12.

Jaman, M. F., Hoque, M. N., Sarker, N. J. and Rahman, M. S. 2012. Ecology and breeding biology of the pond heron, *Ardeola grayii* (Sykes, 1832) and its conservation aspects. – J. Asiat. Soc. Bangladesh Sci. 38: 99–109.

Jovani, R. and Tella, J. L. 2004. Age-related environmental sensitivity and weather mediated nestling mortality in white storks *Ciconia ciconia*. – Ecography 27: 611–618.

Kahl, M. P. 1966. A contribution to the ecology and reproductive biology of the marabou stork (*Leptoptilos crumeniferus*) in east Africa. – J. Zool. 148: 289–311.

Kahl, M. P. 1971a. Food and feeding behavior of openbill storks. – J. Ornithol. 112: 21–35.

Kahl, M. P. 1971b. Observations on the jabiru and maguari storks in Argentina, 1969. – Condor 73: 220–229.

Kahl, M. P. 1972a. Comparative ethology of the Ciconiidae. Part 5: the openbill storks (genus *Anastomus*). – J. Ornithol. 113: 121–137.

Kahl, M. P. 1972b. Comparative ethology of the Ciconiidae. Part 4. The "typical" storks (genera *Ciconia, Sphenorhynchus, Dissoura*, and *Euxenura*). – Z. Tierpsychol. 30: 225–252.

Kahl, M. P. 1972c. Comparative ethology of the Ciconiidae. The wood-storks (genera *Mycteria* and *Ibis*). – Ibis 114: 15–29.

Klosowski, G., Klosowski, T. and Zielinski, P. 2002. A case of parental infanticide in the black stork *Ciconia nigra*. – Avian Sci. 2: 59–62.

Kosicki, J. Z. 2012. Effect of weather conditions on nestling survival in the white stork *Ciconia ciconia* population. – Ethol. Ecol. Evol. 24: 140–148.

Kosicki, J. Z. and Indykiewicz, P. 2011. Effects of breeding date and weather on nestling development in white storks *Ciconia ciconia*. – Bird Study 58: 178–185.

Kosicki, J. Z., Profus, P., Dolata, P. T. and Tobółka, M. 2006. Food composition and energy demand of the white stork *Ciconia ciconia* breeding population. – In: Tryjanowski, P., Sparks, T. H. and Jerzak, L. (eds), The white stork in Poland: studies in biology, ecology and conservation. Bogucki Wyd. Nauk., pp. 16–183.

Kushlan, J. and Hancock, J. A. 2005. The herons. – Oxford Univ. Press.

Lack, D. 1947. The significance of clutch-size. Parts 1 and 2. – Ibis 89: 302–352.

Lekuona, J. M. and Campos, F. 1998. Extra-pair copulations of grey heron *Ardea cinerea* in Arcachon Bay (SW France). – Misc. Zool. 21: 73–80.

Lomnicki, A. 2009. Scramble and contest competition, unequal resource allocation, and resource monopolization as determinants of population dynamics. – Evol. Ecol. Res. 11: 371–380.

Maheswaran, G. and Rahmani, A. R. 2005. Foraging behaviour and feeding success of the black-necked stork (*Ephippiorhynchus asiaticus*) in Dudwa National Park, Uttar Pradesh, India. – J. Zool. 258: 189–195.

Marchant, S. 1988. Nesting behaviour of the Pacific heron *Ardea pacifica*. – Aust. Birds 21: 61–65.

Marchant, S. and Higgins, P. J. 1990. Handbook of Australian, New Zealand and Antarctic birds. – Oxford Univ. Press.

Massemin-Challet, S., Gendner, J. P., Samtmann, S., Pichegru, L., Wulgue, A. and Le Maho, Y. 2006. The effect of migration strategy and food availability on white stork *Ciconia ciconia* breeding success. – Ibis 148: 503–508.

Maust, M., Clum, N. and Sheppard, C. 2007. Ontogeny of chick behavior: a tool for monitoring the growth and development of lesser adjutant storks. – Zoo Biol. 26: 533–538.

[AQ4] Mccrimmon, D. A. Jr, Ogden, J. C. and Bancroft, G. T. 2011. Great egret (*Ardea alba*). – In: Poole, A. (ed.), The birds of North America online. Cornell Lab of Ornithology, <http://bna.birds.cornell.edu/bna/species/570>.

Meanley, B. 1955. A nesting study of the little blue heron in eastern Arkansas. – Wilson Bull. 67: 84–99.

Medeiros, M. J., Emond, E. E. and Ploger, B. J. 2000. An unusual type of sibling aggression in black-crowned night herons. – Condor 102: 438–440.

Miller, L. M. and Burger, J. 1978. Factors affecting nesting success of the glossy ibis. – Auk 95: 353–361.

Mock, D. W. 1985. Siblicidal brood reduction: the prey-size hypothesis. – Am. Nat. 125: 327–343.

Mock, D. W. 1987. Siblicide, parent–offspring conflict, and unequal parental investment by egrets and herons. – Behav. Ecol. Sociobiol. 20: 247–256.

Mock, D. W. 1994. Brood reduction: narrow sense, broad sense. – J. Avian Biol. 25: 3–7.

Mock, D. W. 2006. More than kin and less than kind: the evolution of family conflict. – Harvard Univ. Press.

Mock, D. W. and Parker, G. A. 1986. Advantages and disadvantages of egret and heron brood reduction. – Evolution 40: 459–470.

Mock, D. W. and Lamey, T. C. 1991. The role of brood size in regulating egret sibling aggression. – Am. Nat. 138: 1015–1026.

Mock, D. W. and Forbes, L. S. 1995. The evolution of parental optimism. – Trends Ecol. Evol. 10: 130–134.

Mock, D. W. and Parker, G. A. 1997. The evolution of sibling rivalry. – Oxford Univ. Press.

Moreby, S. J. and Stoate, C. 2000. A quantitative comparison of neck-collar and faecal analysis to determine passerine nestling diet. – Bird Study 47: 320–331.

Nicholson, A. J. 1954. An outline of the dynamics of animal populations. – Aust. J. Zool. 2: 9–65.

North, M. E. 1963. Breeding of the black-headed heron at Nairobi, Kenya, 1958–62. – J. East Afr. Nat. Hist. Soc. 24: 33–63.

Olver, M. D. 1984. Breeding biology of the reed cormorant. – Ostrich 55: 133–140.

Parker, G. A., Mock, D. W. and Lamey, T. C. 1989. How selfish should stronger sibs be? – Am. Nat. 133: 846–868.

Ploger, B. J. and Mock, D. W. 1986. Role of sibling aggression in food distribution to nestling cattle egrets (*Bubulcus ibis*). – Auk 103: 768–776.

Ploger, B. J. and Medeiros, M. J. 2004. Unequal food distribution among great egret *Ardea alba* nestlings: parental choice or sibling aggression? – J. Avian Biol. 35: 399–404.

Quinn, G. P. and Keough, M. J. 2002. Experimental design and data analysis for biologists. – Cambridge Univ. Press.

Redondo, T., Tortosa, F. S. and Arias de Reyna, L. 1995. Nest switching and alloparental care in colonial white storks. – Anim. Behav. 49: 1097–1110.

Romero, J. M. and Redondo, T. 2016. Data from: Kind to kin: weak interference competition among white stork *Ciconia ciconia* broodmates. – Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.XXXXX>. [AQ1]

Roulin, A. 2001. Food supply differentially affects sibling negotiation and competition in the barn owl (*Tyto alba*). – Behav. Ecol. Sociobiol. 49: 514–519.

Roulin, A. and Dreiss, A. N. 2012. Sibling competition and cooperation over parental care. – In: Royle, N. J., Smiseth, P. T. and Kölliker, M. (eds), The evolution of parental care. Oxford Univ. Press, pp. 133–149.

Roulin, A., Colliard, C., Russier, F., Fleury, M. and Grandjean, V. 2008. Sib–sib communication and the risk of prey theft in the barn owl *Tyto alba*. – J. Avian Biol. 39: 593–598.

Roulin, A., Da Silva, A. and Ruppli, C. A. 2012. Dominant nestlings displaying female-like melanin coloration behave altruistically in the barn owl. – Anim. Behav. 84: 1229–1236.

Roulin, A., Des Monstiers, B., Ifrid, E., Da Silva, A., Genzoni, E. and Dreiss, A. 2016. Reciprocal preening and food sharing in

colour-polymorphic nestling barn owls. – J. Evol. Biol. 29: 380–394.

Ryder, R. A. and Manry, D. E. 1994. White-faced ibis (*Plegadis chihi*). – In: Poole, A. (ed.), The birds of North America online. Cornell Lab of Ornithology, <http://bna.birds.cornell.edu/bna/species/130>.

Sasvári, L. and Hegyi, Z. 2001. Condition-dependent parental effort and reproductive performance in the white stork *Ciconia ciconia*. – Ardea 89: 281–291.

Sasvári, L., Hegyi, Z. and Péczely, P. 1999a. Brood reduction in white storks mediated through asymmetries in plasma testosterone concentrations in chicks. – Ethology 105: 569–582.

Sasvári, L., Hegyi, Z. and Hahn, I. 1999b. Reproductive performance of white storks *Ciconia ciconia* breeding at low and high densities. – Folia Zool. 48: 113–122.

Schüz, E. 1943. Über die Jungenaufzucht des Weissen Storches (*C. ciconia*). – Z. Morph. Ökol. Tiere 40: 181–237.

Shaw, P. 1985. Brood reduction in the blue-eyed shag *Phalacrocorax atriceps*. – Ibis 127: 476–494.

Shen, S. F., Chen, H. C., Vehrencamp, S. L. and Yuan, H. W. 2010. Group provisioning limits sharing conflict among nestlings in joint-nesting Taiwan yuhinas. – Biol. Lett. 6: 318–321.

Si Bachir S., Barbraud C., Doumandji S. and Hafner H. 2008. Nest site selection and breeding success in an expanding species, the cattle egret *Bubulcus ibis*. – Ardea 96: 99–107

Singmann, H., Bolker, B. and Westfall, J. 2015. afex: analysis of factorial experiments. – R package ver. 0.13-145, <http://CRAN.R-project.org/package=afex>.

Skead, C. J. 1951. A study of the Hadedah ibis *Hagedashia h. hagedash*. – Ibis 93: 360–382.

Smiseth, P. T. and Amundsen, T. 2002. Senior and junior nestlings in asynchronous bluethroat broods differ in their effectiveness of begging. – Evol. Ecol. Res. 4: 1177–1189.

Snow, B. 1960. The breeding biology of the shag *Phalacrocorax aristotelis* on the island of Lundy, Bristol Channel. – Ibis 102: 554–575.

Thomas, B. T. 1984. Maguari stork nesting: juvenile growth and behavior. – Auk 101: 812–823.

Tortosa, F. S. 1992. Estrategia reproductiva de la cigüeña blanca *Ciconia ciconia*. – PhD thesis, Univ. Córdoba, Spain.

Tortosa, F. S. and Redondo, T. 1992. Motives for parental infanticide in white storks *Ciconia ciconia*. – Ornis Scand. 23: 185–189.

Tortosa, F. S. and Castro, F. 2003. Development of thermoregulatory ability during ontogeny in the white stork *Ciconia ciconia*. – Ardeola 50: 39–45.

Tryjanowski, P. and Kuzniak, S. 2002. Population size and productivity of the white stork *Ciconia ciconia* in relation to common vole *Microtus arvalis* density. – Ardea 90: 213–217.

Tryjanowski, P., Jerzak, L. and Radkiewicz, J. 2005. Effect of water level and livestock on the productivity and numbers of breeding white storks. – Waterbirds 28: 378–382.

Tsachalidis, E. P. and Goutner, V. 2002. Diet of the white stork in Greece in relation to habitat. – Waterbirds 25: 417–423.

Tsachalidis, E. P., Liordos, V. and Goutner, V. 2005. Growth of white stork *Ciconia ciconia* nestlings. – Ardea 93: 133–137.

Urfi, A. J. 2011. The painted stork: ecology and conservation. – Springer.

Werschkul, D. F. 1979. Nestling mortality and the adaptive significance of early locomotion in the little blue heron. – Auk 96: 116–130.

Wright, J. and Leonard, M. L. (eds) 2002. The evolution of begging: competition, cooperation and communication. – Kluwer Academic Publishers.

Zielinski, P. 2002. Brood reduction and parental infanticide – are the white stork *Ciconia ciconia* and the black stork *C. nigra* exceptional? – Acta Ornithol. 37: 113–119.

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