Short Communications

The Wilson Journal of Ornithology 124(2):362–366, 2012

Prolonged Incubation and Early Clutch Reduction of White Storks (*Ciconia ciconia*)

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ABSTRACT.—Two cases of prolonged incubation by White Storks (*Ciconia ciconia*) were observed in the same nest in 2009 and 2010 in southwest Poland. Incubation lasted at least 59 and 65 days, respectively; i.e., 84 and 103% longer than the average incubation period. Extended incubation was accompanied by other abnormal breeding behavior. The lack of observed copulation in either breeding season, an extremely short arrival-breeding interval, and early clutch reduction suggest the eggs were infertile. This is the first record of prolonged incubation in the Ciconiidae, and probably the first record of repeated prolonged incubation by wild birds. *Received 12 September 2011. Accepted 21 December 2011.*

The incubation period is primarily affected by the initial egg mass and speed of embryonic development (Deeming 2002). This period varies little within the particular species in the case of fertile eggs (but see Drent 1975). Occasionally, anomalies in the incubation period occur and the duration may be extended. Prolonged incubation is an instinctive behavior, thought to provide a safety margin for eggs that take longer than normal to hatch (Skutch 1962). However, excessively long incubation periods relate to infertile eggs and the adaptive significance of this behavior is questionable (Afik and Ward 1989, Kloskowski 1999). The duration of incubation should be as short as possible due to energy constraints for the incubating bird (Reid et al. 2002) and increased mortality risk from predators at the nest (e.g., Visser and Lessels 2001, Martin 2002, Weidinger 2002, Miller et al. 2007). It remains unclear why incubating birds fail to recognize infertile eggs. It is also unknown what causes termination of incubation. The secretive behavior of parental birds usually prevents continuous observations, and available accounts on prolonged incubation are based on intermittent visits to the nest by researchers. Thus, it is not known whether extended incubation is preceded or accompanied by other abnormal behavior which could induce prolonged incubation. Moreover, there is no information about an individual bird's tendency to incubate longer than average. To my best knowledge, repeated cases of prolonged incubation in the same nest or by the same individuals have not been previously documented in wild birds.

Prolonged incubation has been recorded for a number of bird species (Holcomb 1970, Sutcliffe 1982, Margalida et al. 2006), but is extremely rare. This phenomenon occurs regularly only in the Procellariiformes (Boersma and Wheelwright 1979, Huin 1997) and occasionally in the Podicipediformes (Kloskowski 1999). An extensive literature search did not locate reliable records of prolonged incubation by White Storks (*Ciconia ciconia*) and other Ciconiidae. One case of this behavior was observed in western Poland in 2011 but exact length of incubation is unknown (Marcin Tobółka, unpubl. data). Possible cases of extended incubation should be much easier to document for White Storks than for other wild birds because it is one of the most popular and charismatic bird species in Europe. The White Stork is exceptionally well studied (reviews in Schulz 1998, Tryjanowski et al. 2006), it nests on easily observed structures (buildings, chimneys, poles), and is subject to restoration projects which include captive breeding (Biber et al. 2003, Olsson 2007). Several dozen stork nests in Europe are monitored on-line with a camera providing continuous data during the course of the breeding season (Dolata 2006). However, in-depth information on incubation behavior of this species is surprisingly scarce. For example, factors affecting the onset of incubation and quantitative contributions of male and female to incubation period are poorly recognized. Little is known on the length of incubation recesses, egg sensitivity to cooling, or egg reduction by parental birds.

The White Stork has biological attributes thought to favor prolonged incubation (but not

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supported by empirical data). These features include: (1) one breeding attempt per year, i.e., birds which cannot renest are under strong reproductive pressure; (2) hatching asynchrony, i.e., naturally wide variation in incubation duration for viable eggs; and (3) low predation risk, i.e., low potential costs of incubation (Marks 1983, Margalida et al. 2006). The absence of reports on prolonged incubation by White Storks and related species, despite the above characteristics, indicate this phenomenon is extremely rare in the Ciconiidae.

I describe two cases, 1 year apart, of prolonged incubation, observed in the same nest of the White Stork. I also describe abnormal behavior of the breeding pair which may help explain the prolonged incubation.

METHODS

Study Species.—The White Stork has one brood per year and the full breeding cycle lasts 16 weeks. The average incubation period is 32 (29–34) days and usually starts with the second egg. Both mates incubate, but the female contributes more than the male. Incubation begins ~2 weeks after arrival of the second partner at the nest. The second partner, usually the female, arrives on average 4.5 days later than the first partner (all data after Schulz 1998, Profus 2006).

Field Procedures.—The extended incubation was observed in 2009 and 2010 in the village of Sieniawka (SW Poland, 50° 46′ N, 16° 46′ E). The location is inside a study plot used for long-term (since 1989) monitoring of the White Stork population. The local population is characterized by one of the lowest stork densities in Poland (1.76 pairs/100 km^2 in 2010) with a continuous decrease in numbers ($\bar{x}$ = 1.4 breeding pairs/yr, 1996–2010), and low reproductive success (Wuczyński 2006a, b). The nest in which the prolonged incubation was observed was on a pole not connected to an electric power line. The first breeding attempt at this site was noted in 1994. The nest location allowed for consistent and repeated observations throughout the breeding season. The conspicuous breeding habit of the White Stork provided a unique opportunity to monitor the behavior accompanying prolonged incubation. The presence of the birds in the nest and their behavior was viewed from the ground several times each day. The area under the nest was inspected for discarded eggs or nestlings. The incubation duration was established based on the behavior of the breeding pair: intermittent attentive periods, turning of the eggs, and parents taking turns incubating the eggs. Initiation of incubation was difficult to ascertain due to long but intermittent periods of sitting on the nest preceding actual incubation. An additional sign of approaching incubation was when the birds began to line the nest. The end of incubation was unambiguously pronounced when the eggs were thrown out, followed by the sudden leaving and long absence of the birds.

OBSERVATIONS

The first partner permanently occupied the nest starting on 18 April 2009, and both partners were at the nest on 19 April (Table 1). One egg was discarded (direct observation) immediately after the second bird appeared at the nest. The minimum clutch size in the 2009 breeding season was four eggs, based on the number of discarded eggs. The latest accepted date for beginning of incubation was 24 April (possibly 1–2 days earlier), as this was the date that a tightly sitting bird was observed. Continuous incubation lasted 59 days until 22 June.

The first arrival date in 2010 was on 29 March and coincided with consistent nest occupation by the first partner. The second bird appeared 14 days later. The start of the incubation period was assumed to be 15 April. Continuous incubation lasted 65 days and finished on 19 June. Two eggs were found under the nest during the course of the breeding season, which was the minimum clutch size.

The contents of the eggs which had been discarded after the end of the incubation period indicated embryo development did not occur in either year. The lack of observed copulations was prominent in both years during the pre-incubation period. Start of incubation was abrupt, soon after the arrival of the second partner.

The length of incubation in 2009 and 2010 was 27 and 33 days beyond the normal incubation period (84 and 103%, respectively). These values could be slightly higher as the precise starting point of incubation was not known. The incubation period was average in the 2001–2008 breeding seasons, when hatching occurred in this nest. The nest was not occupied in 2011.

DISCUSSION

The length of the prolonged incubations observed is within the range reported for other species of birds. Margalida et al. (2006) reviewed

TABLE 1. Reproductive timing of the White Stork in breeding seasons when early clutch reduction was noted, and in two breeding seasons when prolonged incubation occurred (2009–2010).

Breeding variables	2003	2005	2006	2009	2010
First arrival date	5 Apr (2 birds, short visit)	26 Mar (2 birds, short visit)	4 Apr	13 Apr (1 bird, short visit)	29 Mar
Arrival of the first partner (= permanent nest occupation)	14 Apr	15 Apr	4 Apr	18 Apr	29 Mar
Arrival of the second partner	17 Apr	7 May	17 Apr	19 Apr (18 Apr in vicinity)	12 Apr
Incubation period	~22 Apr–25 May	~16 May–19 Jun	?–~4 Jun	~24 Apr–22 Jun	~15 Apr–19 Jun
Eggs or eggshells discarded	19 Apr	7–8 May (2 eggs), 11 Jun	20 Apr, ~26 Apr (2 eggs)	19 Apr, 21 Apr, 15–22 Jun, ~28 Jul	21 Apr, 19 Jun
Last visit at nest	23 Aug	29 Aug	25 Aug	17 Aug	18 Aug

the records of prolonged incubation for 18 species of diurnal and nocturnal raptors. The range of prolonged incubation found was 33–161% in excess of the normal period (the average was 94%). The length of extended incubation in seven nests of the Red-necked Grebe (*Podiceps grisegena*) was 42–50% beyond the average incubation period (Kloskowski 1999). Cases of extremely long incubations were also recorded for the Eurasian Wren (*Troglodytes troglodytes*), 219% in excess of the normal period; European Robin (*Erithacus rubecula*), 243% (Skutch 1962); and Northern Bobwhite (*Colinus virginianus*); 326% (Hernández et al. 2006).

There were behavioral indications suggesting the prolonged incubation in 2009 and 2010 was caused by laying infertile eggs, rather than embryo death. First, there was a distinct lack of copulation by the breeding pairs in both breeding seasons. I did not notice one case of copulating storks at the site throughout the entire breeding seasons in 2009 and 2010, despite intensive observations. The White Stork is a species with a high copulation rate. The average number of copulations reaches ~200 during the breeding season with a frequency up to two times/hr (Tortosa and Redondo 1992, Bocheński and Jerzak 2006). Copulations at this particular nest were regularly observed in previous years, especially in the pre-incubation period.

Second, the period between arrival of the second partner and beginning of incubation was distinctly short in both years. The period amounted to 6 days in 2009, and 3 days in 2010. A reduced arrival-breeding interval is believed to enhance breeding success (Fulin et al. 2009); however, the recorded values were several times shorter than average. It takes 12–13 days on average, before the first egg is laid after the arrival of the second partner to the nest in western Poland (Tryjanowski et al. 2004, Kosicki 2010). The short period between arrival of the second partner and beginning of incubation by the observed storks, may indicate that some eggs were formed before being fertilized, even if both birds were able to breed. However, the lack of copulations in 2009 and 2010 and rapid initiation of breeding imply that at least one bird was immature or infertile, or the pairs were of the same sex. Production of eggs could also be influenced by food stress (Deeming 2002). Insufficient food and low digestive efficiency by the female (Kwieciński and Tryjanowski 2009) may cause breeding stress that leads to production of infertile eggs.

Egg losses for White Storks are usually caused by fights with intruders trying to take over a nest already occupied by a pair (Profus 2006, Tobółka et al. 2011). However, White Stork females may occasionally lay infertile eggs before the male's arrival and then throw them out (Schulz 1998). This happened in 2009; one egg was discarded after the second partner arrived at the nest. Similar clutch reduction occurred soon after arrival of the second partner at this nest in previous years. In 2003, one egg was discarded 2 days after the arrival of the second partner. In 2005, two eggs were discarded up to 1 day after the arrival of the second partner. In 2006, one egg was discarded 3 days after the arrival of the second partner (Table 1). Regular occurrence of early clutch reduction has not been reported for the White Stork. This suggests the nest was repeatedly first

occupied by females, which is also unusual in this species (Bocheński and Jerzak 2006). These observations indicate that early laying of infertile eggs by the White Stork may occur more regularly than believed. It is possible that in some years laying infertile eggs may initiate extended incubation.

It is of interest, that prolonged incubation in the same nest occurred in two consecutive years. It is probable that in both cases, one or both of the birds were the same as the previous pair, in view of the high return rate of White Storks to previous nest-sites (Chernetsov et al. 2006, Vergara et al. 2006). This could not be confirmed as the observed storks were unmarked.

Several phenomenon believed to be rare in birds were documented. To my knowledge, this is the first record of prolonged incubation in the Ciconiidae, and probably the first record of repeated prolonged incubation for wild birds in the same nest. Prolonged incubation was accompanied by other behavioral abnormalities, based on continuous nest observations. The breeding behavior of the parental birds was atypical and finished with nest failures. This suggests prolonged incubation in the observed White Storks resulted from a set of factors, related to individual attributes of the parents which reduced reproductive possibilities. Thus, cases of incubation well beyond the expected hatch date for many species of birds may be associated with abnormality in breeding. Behavior accompanying prolonged incubation is difficult to detect in other bird species, unlike in the White Stork, and may be unnoticed. Further investigation is necessary to understand the regulation of incubation behavior of birds, especially prolonged incubation.

ACKNOWLEDGMENTS

I am grateful to Piotr Profus for help in searching the stork literature, and for contributing to our discussions on the issue. I thank C. E. Braun and two anonymous reviewers for valuable comments on the initial version of the manuscript.

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