Motives for parental infanticide in White Storks *Ciconia ciconia*

Francisco S. Tortosa and Tomas Redondo

White Storks *Ciconia ciconia* parents were observed to kill their smaller chick in 9 out of 63 nests observed during a three-year study. Infanticidal parents were caring for larger broods and laid larger clutches than non-infanticidal birds. Males killed the chick in 8 out of 9 cases. Victims were born from the last-hatched egg in 4- and 5-egg clutches, they were the lightest in their brood and grew at lower rates than their nestmates during the days preceding their elimination. The last-hatched nestlings in 4-chick broods had lower pre-fledging survival rates than their elder sibs. Potential victims contributed a low fraction to parents' reproductive output, and 4-chick broods were especially costly to raise because parents provisioned them both more frequently and for longer nestling periods. Hence, the presence of an extra chick seems to lower the benefit/cost ratio to parents rearing a large brood once its elder siblings have hatched successfully. If nestlings do not compete aggressively for food, parents would be selected to eliminate the extra chick themselves. This hypothesis could provide an explanation for the existence of parental infanticide also in other species.

F. S. Tortosa, Departamento de Biologia Animal, Facultad de Ciencias, Universidad de Cordoba, E-14071 Cordoba, Spain. T. Redondo, Estacion Biologica de Doñana, CSIC, Apdo. 1056, E-41080 Sevilla, Spain, and (present address and for correspondence): Department of Zoology, University of Cambridge, Cambridge CB2 3EJ, UK.

Introduction

Brood reduction (i.e. the death of a fraction of the brood promoted by the remaining family members) is a trait common to several avian taxa, but the evolutionary roles played by parents and the surviving offspring in the elimination of the victims are a matter of controversy (O'Connor 1978, Drummond et al. 1986). Parents have been shown to favour competitive asymmetries among nestmates, e.g. by laying eggs of different sizes which hatch asynchronously (Magrath 1990), and not to interfere with the active elimination of the less competitive chicks by their dominant siblings (e.g. Cattle Egrets *Bubulcus ibis*, Fujioka 1985; Blue-footed Boobies *Sula nebouxii*, Drummond et al. 1986).

When hatching occurs asynchronously, the reproductive value of the last chick often depends upon the fate of its elder siblings (Mock and Parker 1986). Only when the oldest broodmates die or are in poor physical condi-

tion can the last-hatched chicks overcome the competitive disadvantage imposed by a lower degree of sensory-motor development or weight at hatching. Caring for a large brood may have detrimental effects upon adult survival rates (Nur 1988), hence parents (especially those in long-lived species) may not be selected to invest in a current brood at their maximum working capacity (Fujioka 1985). Consequently, they could benefit from the rapid elimination of the less valuable offspring by allowing their better-quality sibs to win in competition for food and so maintain an aggressive dominance hierarchy which may end in siblicide. For example, parents of the siblicidal Blue-footed Booby could easily eliminate their smaller chick, but they do not (Anderson 1991). Instead, they sustain a competitive asymmetry among nestmates, then desist from interfering when sib aggression appears (Drummond et al. 1986).

In a few species, however, it has recently been re-

Table 1. Average reproductive parameters of White Storks during 1990 according to clutch and brood size. *** P<0.001.

	Clutch Size				P[1]
	2	3	4	5	
Number of clutches	4	19	15	6	
Fledglings per clutch (all pairs)	1.00	1.64	2.33	2.71	0.08
Fledglings per clutch (successful pairs)	1.33	2.57	2.80	2.71	<0.05
Number of chicks which starved	0.00	0.00	0.83	2.00	<0.01
Number of infanticidal pairs	0	0	2	4	
Egg mass decline with laying order[2]	−0.25	−0.32	−0.46***	−0.80***	
Hatching asynchrony[3] (d)	0.00	0.80	1.33	2.00	<0.05
Reproductive value (RV) of the last-hatched egg[4]					
"extra" RV	–	0.80	0.27	0.00	
"insurance" RV	–	0.20	0.31	0.00	

	Brood Size				P
	1	2	3	4	
Number of broods	4	4	6	5	
Fledgling body mass (g)	3796	3779	3573	3188	<0.001
Adult feeding rate (trips h^{-1})	0.22	0.32	0.47	0.76	<0.001
Length of nestling period (d)	91.3	89.8	91.3	105.0	<0.01

1. One-way ANOVA, but brood-size effects in a two-way ANOVA (brood-size × age of chicks) for adult feeding rate.
2. Pearson's correlation coefficient between egg mass and laying order.
3. Difference between the last and the first-hatching eggs.
4. Not enough data for 2-egg clutches.

ported that brood reduction was accelerated by direct attacks by the parents on the victimized chicks. Parents have been observed to kill their own chicks in Coots *Fulica atra* (Horsfall 1984), Heermann's Gulls *Larus heermanni* (Urrutia and Drummond 1990), Spoonbills *Platalea leucorodia* (Aguilera 1990), and White Storks *Ciconia ciconia* (Schüz 1984). Deaths always occurred in the first few days after hatching. None of these cases was related to contexts of mate exchanging or male take-overs of breeding females, two situations where the infanticidal adults may enjoy a net gain in expected future reproduction (Hrdy 1979, Fujioka 1986). Parental infanticide might seem paradoxical because a parent that so promptly kills a chick seems to assume, rather than test, the vigour of elder offspring, a problem not faced by parents who allow the death to occur through sibling competition (Urrutia and Drummond 1990).

To reconcile the existence of parental infanticide with the idea that brood reduction is adaptive from the point of view of parents' reproductive interest, we will advance the hypothesis that parental infanticide is restricted to species with non-aggressive young in which the cost of nurturing the extra chick until it is outcompeted by sibs and starves is greater than the expected benefit from allowing it to survive a little longer. A low relative reproductive value of the extra chick is expected in large broods of species in which parents reliably know early on how many nestlings they will be able to raise and in which the successful early development of a hatchling reliably predicts successful development throughout the nestling period. The aim of this paper is to present data on parental infanticide in White Storks which seem to give support to the above hypothesis.

Methods

Data on White Stork reproductive biology were collected during 1987 (14 nests, 705 observation h per brood), 1989 (14 nests, 1058 h per brood), and 1990 (23 nests, 882 h per brood) in three breeding areas of Western Andalusia, Southern Spain. Broods were monitored continuously during five-days-a-week periods from hatching to fledging. Adults were marked with numbered PVC rings. Among most of the unmarked birds, members of the same pair could be distinguished by differences in plumage, body morphology or relative size. Sex was assigned on the basis of copulation behaviour. Groups of nests were kept under observation simultaneously, and behaviour samples collected on an "ad libitum" basis, so that observation durations were the same for all broods in a given year. During 1990, we recorded the laying and hatching order, fresh egg mass and chick mass (at 1- to 6-d intervals) at 35 nests with individually marked eggs and nestlings. Laying and hatching sequence was determined with an accuracy of 24 h. Weighing was performed by means of Pesola

186

Table 2. Change in body mass of White Stork nestlings, expressed as percentage of body mass at hatching, in six broods in which parents killed a nestling (marked with an asterisk) during the 1990 breeding season.

Hatching order	Age of first-hatched nestling (d)					
	3	3	5	5	7	9
1	95	100	150	102	200	1062
2	105	80	125	100	150	471
3	45	89	* 16	116	120	714
4	* 0	0		50	* −5	* 62
5		* −14		* −5		

spring balances. We also recorded parental feeding rates at 19 nests with constant brood size from hatching to fledging as the number of adult visits to the nest ending in food regurgitation. Average pooled feeding rates for male and female parents were computed for the whole nestling period (up to 70 days). We looked for brood-size effects upon parental feeding rates by means of two-way ANOVA (brood size × chick age categorized into blocks of 10 d). Qualitative information on diet composition was gathered by inspecting pellets collected at the nests of both breeding (n = 35) and non-breeding adults (n = 11).

In order to determine whether a sustained period of slow growth affected nestling development irreversibly, nine nestlings which were starving in 4- and 5-chick broods were transferred to 1-chick broods containing a nestling of a similar body mass. We compared the body mass at 60–65 d of transferred nestlings with that of chicks which developed in natural 2-chick broods, as an estimate of asymptotic mass.

Results

We witnessed nine instances of parental infanticide at different nests (1 in 1987, 2 in 1989, and 6 in 1990). In another 16 cases, we observed adults pecking at chicks which had previously died from unknown causes. Parents killed the nestlings by holding their necks in the beak and shaking them violently. Apparently, the nestlings died in a few seconds. All parents (both infanticidal or not) tried to swallow the chick but none was successful, though they consumed the corpse partially. Males killed the chicks in eight out of nine cases (Sign test, P = 0.04). In four cases, the female was present at the time the victim was attacked. On two more occasions, the female landed on the nest while the male was attacking the chick or attempting to swallow it, but in no case did she attack the chick. Two banded males were 4 and 6 years old.

At the time chicks were attacked (before 14 days of age), infanticidal parents were caring for broods larger (4.0 chicks, SD = 0.75, n = 8) than those of non-

infanticidal birds (2.75 chicks, SD = 0.91, n = 32) (t test, unequal variances, t_{13} = 4.0, P<0.001). This was not due to a larger average brood size during 1990 (3.1 chicks), when most cases of infanticide occurred, than during 1987 (2.4 chicks) or 1989 (3.0 chicks) (one-way ANOVA, $F_{2,57}$ = 1.6, NS). In 1990, victimized chicks were born from the largest (4- and 5-egg) clutches. Terminal eggs in these clutches were typically smaller and hatched 1–2 d later (Table 1).

Victimized chicks during 1990 were born from the last (five cases) or the penultimate (one case) eggs. Mock and Parker (1986) have shown that the last chick in asynchronously hatching broods represents two kinds of reproductive value (RV) to the parents: "extra RV" (obtained whenever it survives alongside its elder sibs) and "insurance RV" (obtained where it acts as a replacement if another sib dies first). Calculations of both components of RV for clutches of 3, 4 and 5 eggs according to Mock and Parker's formulas (Table 1) show that last eggs are less valuable the larger the clutch, and that in 4-egg clutches, roughly half of the benefit is due to the "insurance" component. In all cases observed, victimized nestlings were the lightest in their brood, and grew at much lower rates than their nestmates during the days preceding their elimination (Table 2). Out of five chicks that showed zero or negative growth at some point between hatching and 25 days, four were killed by their parents during the period of reduced growth . By contrast, no chick was attacked among the remaining 66 nestlings which showed continuous positive growth (Fisher's test, P<0.001). The age at which deadly aggression took place was 7.3 d (SD = 4.0, n = 9), with a range of 2–14 d. Nestlings killed by their parents died at a younger age than last-hatched nestlings who starved (13.2 d, SD = 6.7, n = 13) (t_{20} = 2.6, P<0.01). Mortality other than predation affected last-hatched nestlings in 4-chick broods disproportion-
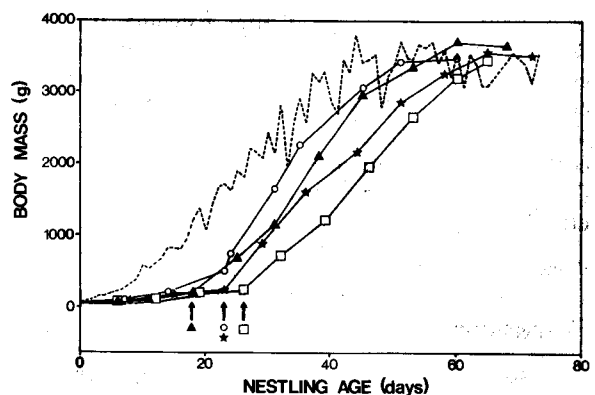

Fig. 1. Growth curves of four White Stork nestlings (each represented by a different symbol) which were starving in their original nest, before and after being transferred to 1-chick broods (continuous lines). Arrows indicate the age of transfer. The growth curve for nestlings in natural 2-chick broods is represented by a dotted line.
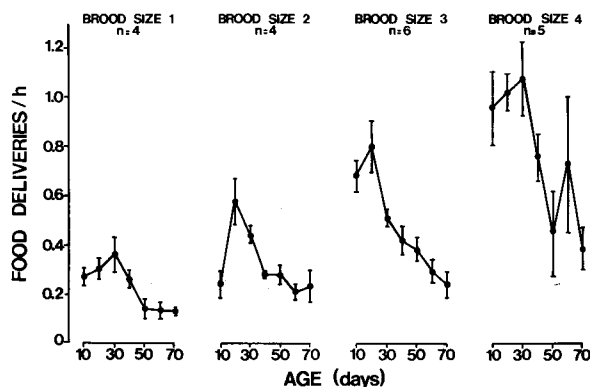
Fig. 2. Average (±SE) rates of food provisioning by White Stork parents to their chicks according to brood size and chick age categorized into blocks of 10 days.

ately. In 15 4-chick broods in which mortality could not be attributed to predation, 12 (80%) of the last-hatched nestlings died prior to fledging. The corresponding figure for senior nestlings was 8/45 (17.8%) ($\chi_1^2 = 16.9$, $P<0.001$).

Starving nestlings showed a remarkable capacity to recover and gain weight provided they received enough food. Fig. 1 shows that chicks which were starving in their original nest had an almost normal growth pattern after they were transferred to 1-chick broods, and reached asymptotic masses similar to those of well-fed chicks in natural 2-chick broods ($t_{19} = 0.17$, NS).

Very young chicks were fed almost exclusively insects (Coleoptera). As nestlings grew older, parents increased the proportion of small crayfish *Procambarus clarkii*. Chicks older than 30 d consumed large crayfish and carps *Cyprinus carpio*. Pellets of non-breeding adults during the same period contained almost exclusively large crayfish and carps.

Rates of food provisioning to the nestlings reached a peak between 20 and 30 d after hatching and then decreased until fledging (Fig. 2). Provisioning rates increased exponentially as a function of brood size, but chicks fledged at significantly lower body masses in 4-chick broods. Chicks fledged asynchronously and, consequently, parents tended larger broods for longer (Table 1). Parents were never observed to feed chicks after fledging.

Discussion

The most productive clutches in our study area were those of 4 and 5 eggs despite the fact that only in these clutches did some nestlings die from starvation or infanticide. This fact might indicate that it pays parents to incubate a large clutch which may subsequently become reduced by the selective death of some nestlings. Extra chicks are given a chance to act as an "insurance"

against the early death of a senior sib. But caring for a large brood may have negative effects on parent residual reproductive value (Nur 1988) and on fledgling quality (because fledging mass decreases with increasing brood size, Table 1). Parents should reduce such negative effects by eliminating extra chicks at an early age if they can predict that such negative effects are likely (e.g. by observing that the last-hatched young is starving and/or they are sensitive to cues indicating that body reserves become exhausted). A similar benefit has been suggested for bird species in which obligate brood reduction is brought about by siblicide (Anderson 1990, Mock et al. 1990). However, an alternative explanation is still possible for the observed correlation between clutch size, brood size and productivity. If better parents lay larger clutches, the higher success of larger clutches might be due to parental quality and not clutch size itself.

When prey delivered to nestlings are small enough to be economically defendable by the eldest offspring, they can monopolize the food and prevent their smaller sibs from feeding by means of agonistic interactions (Mock 1985, Mock et al. 1987, 1990). The way storks feed nestlings, by regurgitating a large amount of food onto the nest, make prey non-monopolizable and no aggression was indeed observed prior to 50 d of age in this or other studies (Schüz 1984). In a similar way, Thomas (1984) reported sibling rivalry in the Maguari Stork *Ciconia maguari* to be "rare and mild". Overt aggression between chicks is also absent in Coots, Heermann's Gulls and Spoonbills, although the ultimate reason for this could vary from one species to another. Another common feature shared by these three species is that the victimized chicks were the smallest in the brood, suggesting that when a chick becomes supernumerary, parents select the least viable one as a victim.

According to the hypothesis proposed here, parents should incur too high a cost for the benefit gained (in terms of chick reproductive value) by allowing potential victims to continue to live. Two previous studies have identified such a cost. In the Coot, potential victims interfered with the efficient prey capture of the adults, which they accompany during foraging (Horsfall 1984). In the Spoonbills, victimized nestling were able to intercept food by inserting their bill into the female's throat while she was feeding another chick (Aguilera 1990).

Nestling White Storks are cared for by both parents until they abandon the nest, at about 70 d of age. Non-breeding adults feed on prey much larger than the prey delivered to nestlings during the first half of the nestling period, which suggests that feeding on small prey is less efficient (Moser 1986). Broods of four nestlings seem to be especially costly to raise because parents must provision them both more frequently and for a longer period until chicks become independent. Nestlings in 4-chick broods fledged at lower body masses than those in smaller broods. The ability of starving

188

chicks to recover when transferred to 1-chick broods suggests that nestlings growing at low rates may not neccessarily starve to death at an early age through competition with their stronger sibs. Consequently, parents allowing low-quality nestlings to stay alive may waste their effort by provisioning them. Parents killed chicks when these were one week old, i.e. before they entered the phase of maximum feeding stress (ca. 20 d), and the survival prospects for elder siblings were fairly high. Recent theoretical models of allocation of parental effort when offspring differ in quality suggest that selective brood reduction can enhance parental fitness if infanticide occurs before substantial resources are committed to offspring (Haig 1990).

In its present form, the hypothesis fails to account for the observed bias in the sex of the infanticidal parent. As in the Coot (Horsfall 1984), infanticidal parents were almost always males (also Schüz 1984). A lower degree of paternity confidence in males is unlikely to be responsible for such bias, unless it could be demonstrated that terminal eggs are more likely to be the result of extra-pair fertilizations. A second possibility could be that costs of nurturing an extra chick are higher for males because they invest more in chick feeding. However, male and female White Storks feed nestlings in roughly equal proportions (average male:female ratio 0.89, unpubl. data) and male Coots indeed take a smaller share of feeding duties than females (Horsfall 1984). A third possibility could be that each victimized nestling contributes a smaller fraction to male than to female lifetime reproductive success, hence the cost/benefit ratio of allowing potential victims to live is higher for males. If lifetime variance in reproductive success is larger for males, so that males of a given age differ in their residual reproductive value, those males with a high reproductive potential would both benefit less from rearing a low-quality chick and incur a higher cost in terms of loss of potential future offspring. Both a male-biased adult sex ratio and male-male competition for resources critical to females would increase the variance in male reproductive success relative to females. Males of both White Storks and Coots are larger than females, this size dimorphism probably being related to the need for males to compete aggressively during early spring for preferred territories (Coots) or nest sites (White Storks) (Cramp and Simmons 1977, 1979). Consequently, male variance in lifetime reproductive success may exceed that of females. This hypothesis predicts that only males with a high potential reproductive success would become infanticidal. Regrettably, we lack data to test this prediction but the possibility for future research is open.

References

Aguilera, E. 1990. Parental infanticide by white spoonbills *Platalea leucorodia*. – Ibis 132: 124–125.

Anderson, D. J. 1990. Evolution of obligate siblicide in boobies. I: A test of the insurance egg hypothesis. – Am. Nat. 135: 334–350.

– 1991. Parent blue-footed boobies are not infanticidal. – Ornis Scand. 22: 169–170.

Cramp, S. and Simmons, K. E. L. (eds.). 1977. The Birds of the Western Paleartic. Vol. 1. – Oxford University Press, Oxford.

– and Simmons, K. E. L. (eds.). 1979. The Birds of the Western Paleartic. Vol. 2. – Oxford University Press, Oxford.

Drummond, H., Gonzalez, E. and Osorno, J. L. 1986. Parent-offspring cooperation in the blue-footed booby (*Sula nebouxii*): social roles in infanticidal brood reduction. – Behav. Ecol. Sociobiol. 19: 365–372.

Fujioka, M. 1985. Food delivery and sibling competition in experimentally even-aged broods of the cattle egret. – Behav. Ecol. Sociobiol. 17: 67–74.

– 1986. Infanticide by a male parent and by a new female mate in colonial egrets. – Auk 103: 619–621.

Haig, D. 1990. Brood reduction and optimal parental investment when offspring differ in quality. – Am. Nat. 136: 550–566.

Hrdy, S. B. 1979. Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. – Ethol. Sociobiol. 1: 13–40.

Horsfall, J. A. 1984. Brood reduction and brood division in coots. – Anim. Behav. 32: 216–225.

Magrath, R. D. 1990. Hatching asynchrony in altricial birds. – Biol. Rev. 65: 587–622.

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

– , Drummond, H. and Stinson, C. H. 1990. Avian siblicide. – Am. Sci. 78: 438–449.

– , Lamey, T. C., Williams, C. F. and Pelletier, A. 1987. Flexibility in the development of heron sibling aggression: an intraspecific test of the prey size hypothesis. – Anim. Behav. 35: 1386–1393.

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

Moser, M. E. 1986. Prey profitability for adult grey herons *Ardea cinerea* and the constraints on prey size when feeding nestlings. – Ibis 128: 392–405.

Nur, N. 1988. The cost of reproduction in birds: an examination of the evidence. – Ardea 76: 155–168.

O'Connor, R. J. 1978. Brood reduction in birds: selection for infanticide, fratricide, and suicide? - Anim. Behav. 26: 79–96.

Schüz, E. 1984. Über Syngenophagie, besonders Kronismus. Ein beitrag zur Ethologie speziell des Weißstorchs. – Ökol. Vögel 6: 141–158.

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

Urrutia, L. P. and Drummond, H. 1990. Brood reduction and parental infanticide in Heermann's gull. – Auk 107: 772–794.