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Brood reduction and parental infanticide — are the White Stork *Ciconia ciconia* and the Black Stork *C. nigra* exceptional?

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Abstract. Brood size in birds is reduced through fatal starvation, siblicide or parental infanticide (killing of own offspring). Both Black and White Storks were observed practising facultative parental infanticide. In the White Stork parents regurgitate large amount of food consisting of many small items on the nest bottom. Chicks pick up food themselves, trying to eat as quickly as possible. No aggression among chicks is observed. As a result monopolisation of food does not occur and elimination of the weakest chick is very ineffective. Sometimes parent storks accelerate brood reduction by killing some of the offspring. Surprisingly, although parental infanticide is a quick and efficient method of brood reduction it is rarely observed, even in species practising it.

Key words: White Stork, *Ciconia ciconia*, Black Stork, *Ciconia nigra*, brood reduction, parental infanticide, siblicide, starvation, mortality

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INTRODUCTION

Infanticide refers to the killing of conspecific young by an adult. First hypotheses explaining infanticidal behaviour involved preventing overpopulation or social pathology. These non-Darwinian explanations were soon replaced by alternative hypotheses. It appeared that cannibalism (e.g. Kovacs & Lydersen 1996) and sexually selected infanticide (Hrdy 1979) explained infanticide in terms of direct benefits the killers derive from their actions. Sexually selected infanticide is usually committed by a new breeding partner (male or female), who kills offspring of the previous resident. Infanticide is clearly adaptive because individuals which replace a previous resident and kill nestlings obtain a breeding opportunity. This type of behaviour has been observed both among Passeriformes (Veiga 1990, Kermott et al. 1991, Robertson 1991, Bańbura & Zieliński 1995) and non-Passeriformes (Fujioka 1986, Emlen et al. 1989).

From the evolutionary point of view equally interesting (or even more) are cases when parents kill their own offspring (parental infanticide). However, due to the rarity of such events, calculations of the balance of costs suffered and benefits gained is much more difficult and parental infanticide still remains a puzzling behaviour for behavioural ecologists. Some cases of parental infanticide, in which a widowed partner kills all of his own offspring, could still be explained in terms of sexually selected infanticide. By committing parental infanticide widowed individuals increase their chances of a successful new breeding attempt. In the Cattle Egret *Bubulcus ibis* a male was observed destroying the egg he sired after his partner was wounded. After having done this, the infanticidal male not only obtained a new partner, but also reused the nest (Fujioka 1986). Also in the European Starling *Sturnus vulgaris* widowed males were observed removing eggs and nestlings they sired from the nests. After the

removal new clutches with new females were laid (Pinxten et al. 1995).

In a majority of bird species brood size in poor feeding seasons is reduced by non-aggressive sibling competition for food, which results in starvation of the weakest nestling. However, in the White Stork *Ciconia ciconia* parents often don't wait till starvation occurs and reduce the family size by killing some of their young. This raises an intriguing question — why do parent birds of so few species enhance brood reduction efficiency by parental infanticide?

FORMS OF BROOD REDUCTION

Partial brood-loss is a common phenomenon among birds (O'Connor 1978, Magrath 1990, Mock & Parker 1997) and may be defined as some, but not all, members of a sibship dying from any and all causes. Within this broad category (Fig. 1) one may find the subset of brood reduction. The term brood reduction means abridgement of family size due to sibling rivalry *per se*. The above definitions were proposed by Mock (1994) to provide a more precise lexicon concerning brood reduction.

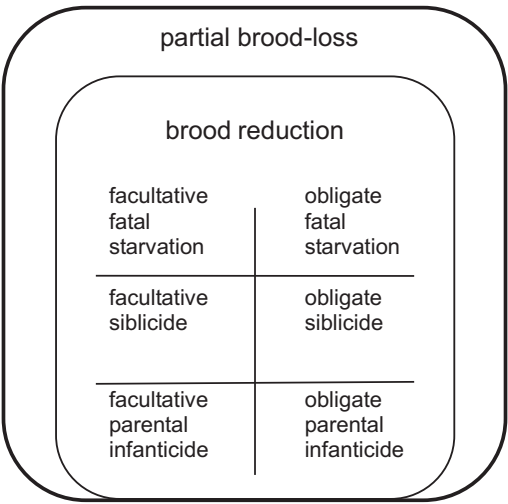


Fig. 1. Partial brood-loss and forms of brood reduction.

We can classify forms of brood reduction according to the frequency of death events across nests (Fig. 1). In facultative brood-reducers handicapped siblings have a reasonable chance of surviving as the elimination of the weakest nestling occurs only when food is limited. In obligate

brood-reducers the death of one sib is almost guaranteed (e. g. in 90% of nests: Simmons 1988, Mock & Parker 1997). Marginal chick survives only if the older sibling fails to hatch or dies at an early age.

We can further classify brood reduction systems according to the immediate cause of nestling death (Fig. 1). Both in facultative and obligate brood-reducers one can distinguish the following causes of nestling death: fatal starvation — brood reduction resulting from non-aggressive sibling rivalry, siblicide — killing the weaker sibling, parental (filial) infanticide — selective killing of some of own offspring (excluding whole brood abandonment).

Facultative selective starvation is by far the most common form of brood reduction in birds (Lammey & Mock 1991, Mock & Parker 1997). It was observed for example in the Blackbird *Turdus merula*; in this species brood reduction through nestling starvation was common only in poor feeding seasons (Magrath 1989). In facultative siblicide systems chicks adjust fighting rate to feeding conditions, with fatal consequences for younger nest-mates when food is scarce. In Ospreys *Pandion haliaetus* chicks are more aggressive towards siblings when hungry and in nest when food was limited aggression accounted for the preferential feeding of older nestmates (Poole 1982, Forbes 1991). Not only predatory birds, well equipped with weaponry specialised for fights, practice siblicide. In the Blue-throated Bee-eater *Merops viridis* the smallest nestlings are sometimes killed by their larger siblings with a sharp hook, downward pointing, placed at the tip of the upper mandible. The interesting thing is that the hook is lost later in the nestling period (Bryant & Tatner 1990). In facultative parental infanticide systems parents sometimes actively kill an inferior chick. Direct killing of some of the young was observed for example in the White Stork (Tortosa & Redondo 1992) and in the Black Stork *Ciconia nigra* (Kłosowski et al. 2002).

In obligate brood-reducers family size is decreased by fatal starvation of the weakest chick, siblicide or parental infanticide. In the case of obligate starvation to death, no aggressive sibling competition or parental infanticide occurs and the smaller chick virtually always dies of hunger, which was observed in Fjordland Penguin *Eudyptes pachyrhynchus*, Rockhopper Penguin *E. chrysocome* and Snares Penguins *E. robustus* (Lamey & Mock 1991, Lamey 1993).

In obligate siblicide systems one sib is almost always murdered early in the nesting period by

the stronger chick, with no parental interference. The Black Eagle *Aquila verreauxi* is a classical example of a species that practises obligate siblicide with only one chick surviving to fledging (Simmons 1988).

Obligate parental infanticide was observed in Royal Penguins *Eudyptes schlegeli*. In this species mothers actively reduce brood size by ejecting the smaller first egg (St Clair et al. 1995). Parental egg ejection early in the breeding period, when competition among siblings is completely absent, decreases the future sibling competition. Thus it can also be regarded as a form of brood reduction. Both obligate fatal starvation and obligate parental infanticide are rare forms of brood reduction in birds (Mock & Parker 1997). However, it should be noted that the above forms of brood reduction are not mutually exclusive. In many cases death occurs as a joint effect of siblings or parents aggression and underfeeding.

PARENTAL INFANTICIDE IN BIRDS

In a majority of bird species parents participate in brood reduction only indirectly by providing food to the most vigorously begging nestlings placed in preferable (relative to the parent) positions (McRae et al. 1993, Godfray 1995, Kilner 1995, Kilner & Johnstone 1997). Rarely do parents intervene actively and reduce brood size by killing or even cannibalising the weakest nestling (Bortolotti et al. 1991, Stanback & Koenig 1992, Mock & Parker 1997). Occasional parental infanticidal behaviour has been also observed in the Roadrunner *Geococcyx californianus* (Ohmart 1973), Coot *Fulica atra* (Horsfall 1984) and Heerman's Gull *Larus heermanni* (Urrutia & Drummond 1990). Probable cases of parental infanticide were recorded in the House Sparrow *Passer domesticus* (Long 1966) and in the Tree Sparrow *Passer montanus* (Pinowski 1968, J. Pinowski — pers. comm.).

Among Ciconiiformes parental infanticide has been observed in two families: Threskiornithidae and Ciconiidae. In the White Spoonbill *Platalea leucorodia* (Threskiornithidae), in the nest observed, both parents repeatedly attacked the youngest chick in the nest without feeding it at all which together resulted in victim's death (Aguilera 1990).

In the stork family Ciconiidae parental infanticide has been reported in the White Stork (Tortosa & Redondo 1992) and in the Black Stork *Ciconia*

nigra (Kłosowski et al. 2002). However, parental infanticide has not been observed in the Maguari Stork *Ciconia maguari* (González 1998) and in the Wood Stork *Mycteria americana* (González 1999).

PARENTAL INFANTICIDE IN THE WHITE STORK

White Storks are monogamous. They breed either solitarily or in colonies, usually lay clutches of 4 (range 1–7) eggs and raise one brood in the breeding season. Eggs are laid at intervals of 1–4 days, mostly two and incubation starts with the second egg and usually lasts 32 days. Hatching is asynchronous and chicks fledge at age 54–68 days (Schultz 1998).

Lack (1947, 1966) predicted that the best strategy for altricial birds with a long period of clutch occupation faced with food unpredictability might be to lay an optimistic clutch size and to start incubation before clutch completion. As a result, in asynchronous broods enduring a food shortage only some instead of all of the young die. The weakest nestling survives and fledges only when food is abundant. Since the White Stork is a semi-altricial species with a long fledging period, it almost perfectly fits these predictions. Food provisioning activity to the White Stork nestlings is highest between 20 and 30 days (Tortosa & Redondo 1992). So the time between the moment of fertilisation and the time of the highest nestling demands is well over two months (pair formation + incubation + 20–30 days) and because of the length of this period resource availability predictions at the time of laying are likely to be inaccurate. As incubation starts with the second egg, hatching is asynchronous and the age differences between the youngest and the eldest nestlings in large broods might even be ten days (Haverschmidt 1949, Cramp 1977). However, in the White Stork parents occasionally actively reduce brood size themselves instead of waiting for the death to occur later through sibling competition. They do it by throwing out of the nest eggs or by killing and cannibalising or throwing chicks out of the nest (Wodzicki 1877, Schüz 1957, Borowski 1963, Meybohm & Fiedler 1983, Jakubiec 1991, Tortosa & Redondo 1992). The frequency of this phenomenon varies between years. In a Spanish population Tortosa & Redondo (1992) monitoring continuously the behaviour of marked adult White Storks recorded parental infanticide at one nest out of 14 in 1987 and at six out of 23 in 1990. It is the only species in which facultative parental infanti-

cide has been documented so widely. Infanticidal behaviour in the White Stork has been observed in different areas of the White Stork's distribution range (Spain, Germany, Poland), in different years and in both colonial and solitarily nesting birds (Schüz 1957, Borowski 1963, Meybohm & Fiedler 1983, Jakubiec 1991, Tortosa & Redondo 1992).

PARENTAL INFANTICIDE IN THE BLACK STORK

In the Black Stork a clear case of facultative parental infanticide was recorded in the Łochowskie Forest, eastern Poland (Kłosowski et al. 2002). In the nest observed, a parent black stork regurgitated food consisting of many small items into the middle of the nest. Five chicks quickly swallowed all the regurgitated food from the nest bottom. No aggression was observed between the siblings while feeding. Shortly after feeding the parent bird seized the head of the smallest chick with the bill and threw the chick, which was still alive, out of the nest. The chick was killed by the fall to the ground. There were still some small fish in the throat of the killed chick, proving that it managed to take some food during the last feeding. The remaining four chicks eventually fledged successfully from this nest in the second half of July (Kłosowski et al. 2002).

The Black Stork is a rare species breeding as single pairs in old forests. Thus it is very difficult to observe many nests of this species continuously. As a consequence no data are available on the frequency of infanticidal behaviour in this species.

CAUSES OF PARENTAL INFANTICIDE

Parents overproducing zygotes should be able to identify and eliminate offspring with the lowest fitness expectations as early as possible (Kozłowski & Stearns 1989, Konarzewski 1993, Mock & Forbes 1995). Indeed, in all cases observed in the Tortosa & Redondo (1992) study, victimised chicks were the lightest in their brood and grew at much lower rates than their nest-mates. The average nestling age at which deadly aggression took place was 7.3 days, so quite early in the nestling period (Tortosa & Redondo 1992).

A possible explanation for the high incidence of parental infanticide, rather than siblicide, is connected with the way in which parents feed their young. Parent White and Black Storks regurgitate large food boluses consisting of many small

items into the middle of the nest. Chicks sit in a circle around the downwards-pointed beak of the parent waiting for the food to fall down. When at last the food comes down, it is very quickly swallowed by the young. Even the youngest chick picks up regurgitated food itself from the nest bottom (Haverschmidt 1949, Kahl 1972). Monopolisation of food bolus is not possible as it is too large. In accordance with the prey-size hypothesis (Mock 1985) nestling aggression is low at this stage (Tortosa & Redondo 1992, Redondo et al. 1995) and instead of fighting chicks simply eat as fast as possible. Older chicks try to hold the parent's beak and peck the food out of the parent's throat as soon as it becomes visible. But they are still unable to monopolise the whole bolus of food and only a few pieces are taken directly from the parent's beak before the greatest part of food is regurgitated on to the nest. Superior position in the nest also does not enable the chick to monopolise the food because chicks are in a circle and food is regurgitated into the middle of the nest. It may be that the inability of individual chicks to monopolise resources prevents siblicide, thus forcing brood reduction through parental infanticide. Tortosa & Redondo (1992) advocate the hypothesis that if nestlings do not compete aggressively for food, parents should be selected to eliminate the surplus chick themselves.

An additional egg or chick represents two kinds of reproductive investment. In the case of "extra reproductive value" marginal chicks survive in addition to all their siblings, which is most likely to happen during favourable seasons. In "insurance reproductive value" the extra chick serves as a replacement for an older sibling that dies prematurely (Konarzewski 1993, Mock & Forbes 1995). Both kinds of reproductive values are represented in the White Stork (Tortosa & Redondo 1992), though the relative contribution of the two forms is difficult to assess in practice because parents sometimes throw single eggs out of the nest early in the nestling period and sometimes some or even all eggs are destroyed by foreign adult Storks (Haverschmidt 1949, Jakubiec 1991). The interesting observation is that in some detailed studies on the White Stork breeding biology parental infanticide was never observed. Infanticidal behaviour was not recorded during a three year study of the White Stork breeding at both low and high density (Sasvári et al. 1999a, 1999b). Thus further detailed studies are necessary to explore the relationship between frequency of infanticide, parental quality and feeding conditions.

Brood reduction is not always associated with food shortage. According to Simmons (1988), in saturated large raptor populations, selection for high-quality, competitive offspring is likely to overshadow selection for large brood size, even in the absence of food stress. As a result the successful young may fledge at a higher weight, thus enhancing its future chances of acquiring a breeding territory.

Brood reduction due to parental infanticide was also observed in mammals though because of its cryptic nature the frequency of this behaviour in birds and mammals is probably underestimated (Clutton-Brock 1991, Mock & Parker 1997).

BROOD REDUCTION AND PARENTAL HORMONAL FAVOURITISM IN WHITE STORKS

Parental infanticide is not the only mechanism of adjusting brood size to feeding abilities. A new study of White Storks by Sasvári et al. (1999a) has shown that one maternal effect — the plasma testosterone concentrations in chicks, transmitted from the mothers via their eggs — could have a remarkable influence on offspring survival. Sasvári et al. (1999a) compared broods of White Storks where chicks died with those where all chicks survived and analysed the plasma testosterone concentration in the chicks, their vigour and hatching order. It was found that highest testosterone levels were recorded in the first chick to hatch and the lowest in those chicks that hatched last. However, the plasma testosterone levels of the first-hatched chicks were higher in broods where chicks died than in broods where all the chicks survived. First-hatched chicks responded faster to the arrival of the parents with food and received most food, while last-hatched chicks responded slower and received less food. Sasvári et al. (1999a) showed that females in poor condition altered the plasma testosterone concentrations to produce large differences between the chicks. Females in good condition produced small differences in testosterone concentrations between the chicks and all chicks survived in their brood. Thus, females of poor condition accelerate brood reduction by transmitting strong asymmetries in testosterone concentrations into the offspring while females of good condition transmit low asymmetry of testosterone concentration to the chicks because they are able to raise offspring without brood reduction (Sasvári et al. 1999a). Also in the Cattle Egrets *Bubulcus ibis* mothers deposit more androgens in the first eggs of their clutches, adding

a potential hormonal boost to first-hatched chicks. This may help older offspring to eliminate younger nest-mates (Schwabl et al. 1997).

CONCLUDING REMARKS

The avian family Ciconiidae is a distinctive family comprising 19 species (Slikas 1998). However, detailed comparative behavioural data concerning the mechanism of brood reduction in the family Ciconiidae are not yet available.

Lack of aggression among the White Stork siblings at the early stage of nestling development (Tortosa & Redondo 1992, Redondo et al. 1995) may explain why parent storks accelerate brood reduction by infanticide. In the majority of other species with asynchronous hatching parents leave the job of brood reduction to competing nestlings, thus suffering the additional cost of providing the food to all the chicks until, in the case of food shortage, the weakest are outcompeted by the stronger sibs. However, it should pay parents to employ both strategies. The low frequency of recorded parental infanticide among species does not support this view. So either the frequency of parental infanticide is underestimated in the literature or the benefits from brood reduction through infanticide are only high enough in species, in which sibling competition does not skew the distribution of food to particular offspring.

Another possible explanation is that, generally, parents of any species are aware of their ability to reduce family size by parental infanticide. Usually they don't do it because in most cases the offspring competition is efficient in adjusting the final brood size to the parents' capability. Very rarely external conditions and breeding biology of the species favour parental infanticide. However, if it was possible to cause brood destruction through parental infanticide experimentally (e.g. Pinxten et al. 1991), it should be also possible to experimentally cause brood reduction due to parental infanticide. By manipulating brood size, food level, chick condition and aggression it should be possible, at least in some species, to create situation where brood reduction by parental infanticide would occur.

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STRESZCZENIE

[Redukcja lęgu i zabijanie potomstwa — czy bocian biały i bocian czarny są wyjątkowymi przykładami tego zjawiska?]

Częściowa utrata lęgu może być wynikiem redukcji lęgu, związanej z konkurencją między pisklętami, lub też może być wynikiem innych czynników np. drapieżnictwa. Redukcja lęgu u ptaków może odbywać się w różny sposób. Najślabsze pisklę może zostać zagłodzone na śmierć (fatal starvation), może być zabite przez rodzeństwo (siblicide) lub przez jednego z rodziców (parental infanticide). Procesy te mogą być fakultatywne lub obligatoryjne (Fig. 1). Zabijanie własnego potomstwa, bardzo interesujące z ewolucyjnego punktu widzenia, jest rzadko obserwowaną formą dzieciobójstwa. Poprzez

wybiórcze usuwanie z lęgu najślabszych piskląt osobniki rodzicielskie mogą przyspieszyć proces redukcji lęgu, oszczędzając w ten sposób zasoby konsumowane przez pisklę o bardzo małych szansach przeżycia. Fakultatywne zabijanie potomstwa zaobserwowano, między innymi, u bociana białego, bociana czarnego, warzęchy, łyski, kukawki kalifornijskiej i mewy śniadej.

Zabijanie potomstwa poprzez wyrzucanie z gniazda jaj lub piskląt najczęściej obserwowano u bociana białego, co może jednak wynikać ze znacznie szerszego, w porównaniu z innymi gatunkami, zakresu badań nad tym gatunkiem. U bociana białego agresja pomiędzy pisklętami z jednego lęgu jest bardzo słaba lub nie obserwuje się jej wcale i konkurencja o pokarm polega głównie na jak najszybszym zjedzeniu przyniesionego przez rodziców pokarmu. Ponadto ptaki rodzicielskie wymiotują całą zawartość wola na dno gniazda, a pisklęta samodzielnie pobierają przyniesiony pokarm. Nie następuje więc wybiórcze karmienie poszczególnych piskląt małymi kęsami pokarmu, tak jak to się dzieje u wielu gatunków ptaków drapieżnych. Nie dochodzi do przejmowania zasobów pokarmowych przez najstarsze pisklęta i w efekcie eliminacja najślabszych piskląt rozciąga się na długi okres czasu i przebiega mało skutecznie. Dorosłe bociany często same redukują wielkość lęgu, wyrzucając „nadliczbowe” jaja lub pisklęta. Skoro redukcja wielkości lęgu dokonywana przez ptaki rodzicielskie może być tak szybka i skuteczna, zastanawiające jest, dlaczego dopasowywanie wielkości lęgu do aktualnych możliwości osobników rodzicielskich poprzez zabijanie potomstwa jest tak rzadkie u innych gatunków ptaków.