

Nest switching and alloparental care in colonial white storks

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Abstract. White stork, *Ciconia ciconia*, chicks were observed to abandon their natal nests prior to independence and to be adopted by neighbouring foster parents in approximately 40% of broods at three breeding colonies. Nest switching coincided with a decrease in feeding rates by parents and an increase in aggression by siblings triggered by the flight exercises of nestmates, and mainly affected the eldest chicks in larger broods. Chicks that abandoned their natal nests moved into broods containing both fewer and younger chicks, and thus experienced a decrease in aggression rate compared with their natal broods. Adopted chicks may also have increased their food intake as a consequence of nest switching. Resident chicks suffered from lower feeding rates during adoption and had lower mass increments than chicks in non-fostering broods of comparable age and size. Both adults and chicks were highly aggressive against trespassing chicks. The probability of aggression was a good predictor of the extent of fostering across different brood sizes, suggesting that defence by residents was effective at preventing adoption. Residents appeared not to recognize kin but were capable of aggressive discrimination against non-familiar chicks. Fostering behaviour in this species can be understood as the equilibrial outcome of an intraspecific 'co-evolutionary' arms race between kleptoparasitic chicks and fostering host adults with weak selection pressures for both parties.

Alloparental care (i.e. care of young by a conspecific other than its genetic parent) is widespread in social birds and mammals and includes a range of behaviour from brood amalgamation in precocial birds to babysitting in primates (Riedman 1982; Packer et al. 1992). This phenomenon has attracted much attention because its occurrence apparently violates the Darwinian principle by which animals are selected not to expend resources in the propagation of competing genotypes (Holley 1981; Riedman 1982; Carter & Spear 1986).

One interesting form of alloparental care is nest switching by young birds which actively abandon their natal nests to seek temporary or full adoption by foster parents. Nest switching has been mainly documented in semi-precocial species of colonial seabirds such as gulls and terns, but evidence is now accumulating that it also occurs in fledglings of altricial species such as raptors, egrets and herons (see references below). Chicks seem to benefit from switching to nests where they receive better care (e.g. food) than at their natal nests (Hebert 1988). It is less clear, however, why foster

parents should tolerate the presence of an unrelated chick in their brood. Some instances of alloparental care may be the result of reproductive errors or maladaptation arising from human interference (Plissner & Gowaty 1988; Bustamante & Hiraldo 1990). This explanation, however, fails to account for the high frequency of fostering observed in some species and also for the active role played by young seeking adoption (Holley 1981; Pierotti 1988), especially when they risk being attacked and killed by unrelated adults (Pierotti 1988; Morris et al. 1991). At least in some species (e.g. fully precocial birds), adoption may entail negligible costs, exerting a neutral effect on adult reproductive success (Patterson et al. 1982; Eadie et al. 1988; Bustnes & Erikstad 1990). Alternatively, even if adoption were costly to foster parents, they could obtain some compensating direct benefits, such as gaining reproductive experience or exploiting foster young (e.g. by diluting the risk of predation; Riedman 1982; Birkhead & Nettleship 1984; Eadie et al. 1988). In addition, alloparents may obtain indirect benefits through kin selection (if adopted young are close

relatives; Waltz 1981) or reciprocal altruism (if alloparenting is reciprocated by the adoptee's genetic parents; Pierotti 1980, 1982, 1988, 1991).

These explanations can hardly account for the occurrence of nest switching and alloparental care in colonial birds (Graves & Whiten 1980; Holley 1981; Pierotti 1988). First, it is unlikely that the presence of an alien chick has neutral effects in species providing intensive depreciable parental care (e.g. food provisioning; Pierotti & Murphy 1987; Hebert 1988; Morris et al. 1991). Even if the number or quality of the foster parents' brood are not reduced, they will waste time and energy looking after unrelated young. Second, foster parents appear to benefit little, if at all, from adopting a strange chick (Waltz 1981; Pierotti 1982, 1991; Pierotti & Murphy 1987; Hebert 1988). Adults in these species, and sometimes chicks as well, actually attempt to prevent adoptions by aggressively discriminating against unrelated chicks approaching the nest (Pierotti 1991).

When adoption is disadvantageous to foster parents, it is functionally analogous to brood parasitism (Redondo 1993). Brood parasites and their hosts are engaged in a co-evolutionary arms race in which parasitism selects for defensive strategies in the host (e.g. egg discrimination, nest guarding), which in turn select for counter-defences by the parasite (e.g. egg mimicry, secretive laying behaviour; Rothstein 1990; Petrie & Møller 1991). There is an important difference, however. Brood parasites lay propagules (eggs) in the host nest while, by nest switching, the propagule (chick) places itself in the foster nest. This raises the question of why a chick, which (unlike obligate parasites) is being cared for by its own parents, and (unlike eggs) is able to make a choice, abandons its natal nest to risk both the uncertainty of finding a suitable foster parent and the probability of being attacked by non-relatives.

Pierotti & Murphy (1987) developed a hypothesis to explain the existence of nest switching and alloparental care in colonial birds based upon the arms-race concept. According to this 'inter-generational conflict' hypothesis, chicks receiving inadequate care from their genetic parents are selected to abandon their natal nests to seek adoption. This creates a selective pressure for adults to discriminate against strange wandering chicks and these are, in turn, selected to overcome such defences. When defences by foster parents

(hosts) are not completely cost-free (Redondo 1993), chicks are expected to win the arms race (i.e. to become adopted) for two reasons. First, the selective pressure for the chick gaining acceptance is stronger (surviving versus dying) than for the parent to discriminate against the chick (saving versus losing some of its lifetime reproductive effort; Pierotti & Murphy 1987). Second, if two traits (one promoting adoption in the chick and the other preventing it in the adult) have similar effects on fitness and at least one trait acts within the reproductive period, selection will act more strongly on the trait expressed earlier in life (Charlesworth 1980; Pierotti 1991). A similar argument was employed by Dawkins & Krebs (1979) to account for the lack of effective discrimination against interspecific brood parasites.

In this paper we report a detailed observational study of nest switching and alloparental care in an altricial species, the white stork, *Ciconia ciconia*. The occurrence of nest switching has been reported in different populations of white storks when pairs nest gregariously (Haas 1963; Schmitt 1967). Our aim was to test whether the arms-race concept provides a satisfactory explanation for nest abandonment by chicks and fostering by unrelated adults by analysing the possible costs and benefits of fostering for both parties.

METHODS

Data were collected during 1990 and 1991 at three breeding colonies in Andalusia, Southern Spain, containing, respectively, 8, 12 and over 100 pairs. In the largest colony, we selected a focal sample of 23 nests in the densest part of the colony. In addition, we observed eight isolated nests for comparative purposes, along the margins of the Guadalquivir River and at least 5 km from each other. All breeding adults were individually recognized by means of numbered PVC rings, plumage dyeing or distinctive anatomical features. The sex of adults was determined on the basis of copulation behaviour. All chicks were marked with numbered PVC rings below 50 days of age. Further details on study areas and identification methods are given elsewhere (Tortosa & Redondo 1992a). Chick body mass was recorded every 5–7 days with Pesola spring balances from hatching until fledging.

Continuous observations from dawn to dusk were performed at distances from 10 to 70 m

with the aid of telescopes. We used continuous sampling of focal animals to determine rates of food provisioning by adults, flight exercises by fledglings and aggression against chicks. The location of each bird in the colony was determined by collecting scan samples every 15 min. Definitions of behavioural categories were as follows. Food provisioning involved adults flying to the nest and regurgitating food. Different regurgitations within the same feeding trip were counted as a single feeding. The time elapsed from the arrival of a parent to a nest and food regurgitation was measured with a stopwatch. Rates of flight exercises were determined as the number of take-offs per unit time, regardless of whether chicks abandoned the nest surroundings. Aggression was defined as pecking at another chick's body. Aggression by adults or chicks against other chicks usually took the form of short bouts following landing attempts by the target chick. These aggressive bouts, like feeding episodes, involved much confusion, which precluded calculations of individual aggression or feeding rates by resident chicks. Consequently, we computed two measures of aggression: the number of aggression bouts against resident chicks per unit time and the percentage of landing attempts by a chick on a nest that were aggressively contested by residents. An adoption was assumed to occur whenever a chick that had switched to a foster nest was observed to feed at this nest for at least 1 day.

We were interested in testing whether food provisioning or aggression by residents was responsible for the observed patterns of adoption. Both aggression and food provisioning rates varied according to brood size, so we tested this by analysing the extent of fostering across different brood sizes. Since not all brood sizes were equally abundant, we calculated an index of differential use of broods by wandering chicks as the difference between the observed minus the expected frequency of occurrence of fostering divided by the square root of expected frequency for each brood size category.

To detect whether the presence of adopted young affected the growth of resident chicks, we calculated the increment in body mass of chicks between two measuring points: (1) immediately before adoption took place and (2) 5–7 days afterwards. Mass increments were expressed as a percentage of initial body mass. Such mass increments were compared with those of chicks in

non-fostering broods during the same age period (50–60 days). White stork chicks at this age have usually reached asymptotic body mass and may lose mass, particularly in large broods. For some unknown reason, chicks in four non-fostering nests were still growing actively at 50–60 days. These nests were atypical in showing all the mass gains during this period. Since taking them into account would bias any estimate of mass gain by chicks in non-fostering broods, we excluded them from analyses to make the test more conservative (including them does not alter the conclusions, but lowers the *P*-value in Table V). Mass increments varied according to hatching order and age of initial measurement, but not according to the age span (5–7 days) between measurements. Accordingly, we tested the effect of adoption upon mass increments by removing variation arising from hatching order and age of initial measurement with an analysis of covariance (Zar 1984). As this was a non-experimental procedure, we also compared the relative growth of the same nests between 40 and 50 days to make sure that any effect detected was not due to pre-existing differences between groups.

We found no significant differences between colonies in the percentage of abandoned nests, the percentage of adopted chicks, the percentage of fostering nests, the duration of adoption, the age of the adopted chick, the age of the fostering brood, aggression rates by either parents or resident chicks against either resident or alien chicks, and the percentage of landing attempts by either resident or alien chicks that were aggressively contested by either adults or resident chicks. Consequently, we pooled all data from the three colonies in order to increase sample sizes. Statistical analyses were performed according to Zar (1984). All test probabilities are two-tailed.

RESULTS

During the nestling period (up to 90 days), white stork chicks are provisioned by both parents with food regurgitated on to the nest until they become fully independent since parents do not feed fledglings outside the nest. Offspring independence is a gradual process. Chicks are increasingly capable of performing flight exercises as they get older, and these flights become more frequent and over larger distances until the chick no longer returns

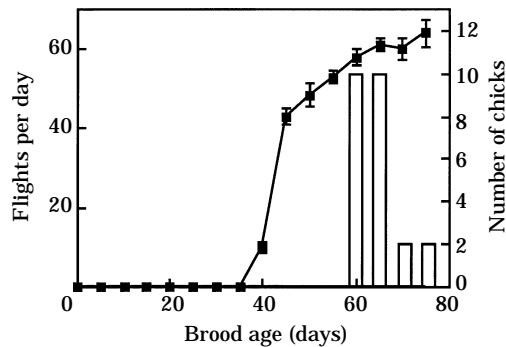


Figure 1. Mean (\pm SE) daily rates of flight exercises by white stork chicks (\blacksquare , $N=45$) and the number of chicks that abandoned their natal broods and were adopted by foster ones (\square , $N=24$), plotted against the age of the brood.

to its natal nest. Chicks that abandoned their natal nests, switching to foster ones, did so around the phase of intense flight exercise (Fig. 1).

Nest switching affected a considerable proportion of nests within a colony. Out of 45 broods observed, 24 (53%) were abandoned by at least one fledgling (range 44–66%) while 20 (44%, range 42–50%) eventually adopted a fledgling that had abandoned its natal nest. Four nests adopted more than one fledgling (two simultaneously, and two sequentially). In those cases where the age of adults was known, the genetic parents were 3.8 years old (± 0.65 SE, $N=5$) while foster parents were 4.0 years old (± 0.53 , $N=9$). The average duration of fostering was 4.3 days (± 0.81 , range 1–14 days, $N=24$). The duration of fostering was not affected by the age of the fostering brood (Spearman $r = -0.29$, $N=24$, NS). However, there was a non-significant trend for older alien chicks to remain at the foster nest for a shorter period (Spearman $r = -0.39$, $N=24$, $P=0.06$). Of the

fledglings successfully adopted 58% never returned to their natal nests and only four were observed to be fed occasionally at their natal nests after having been adopted at foster ones. This suggests that most chicks that switched to foster nests actually reached independence in them.

Proximate Factors Causing Nest Abandonment

One of the predictions of the 'inter-generational arms race' hypothesis is that chicks that abandon nests receive substandard parental care in them (Pierotti & Murphy 1987). We tested this prediction in two ways. First, we predicted that chicks in broods where at least one chick gained adoption at a foster nest were receiving less food than chicks in broods that were never abandoned. In white storks, the amount of food 'per capita' is brood-size dependent, so that chicks in larger broods received less food (Tortosa & Redondo 1992b). This would predict a higher incidence of nest abandonment in larger broods, as indeed occurred (Table I), but other explanations can also account for this pattern (see below). In addition, we expected that adopted chicks would come from undernourished broods. However, 'per capita' rates of parental provisioning between 50 and 70 days were similar in abandoned broods ($\bar{X} \pm \text{SE} = 0.07$ feedings/chick per h ± 0.006 , $N=12$) and in comparable non-abandoned broods, that is those for which suitable foster nests (those containing younger broods less than 20 m apart from the focal nest) were available (0.09 ± 0.008 , $N=7$; Mann-Whitney test: $z=1.2$, NS). Second, we predicted that chicks that abandoned their natal nests would be smaller than the average of their siblings because in white stork chicks a large size confers an advantage during episodes of intra-brood competition for food (Kahl 1972). Contrary to

Table I. The occurrence of nest abandonment across different brood sizes

	Brood size			
	1	2	3	4
Number of broods	8	11	16	7
Number of broods abandoned*	0	5	9	6
Number of abandoning chicks per brood ($\bar{X} \pm \text{SE}$)†	0.0 \pm 0.0	1.0 \pm 0.0	1.1 \pm 0.12	1.7 \pm 0.21

*Chi-squared: $\chi^2=11.8$, $df=3$, $P<0.001$.

†One-way ANOVA: $F_{1,16}=5.34$, $P<0.05$.

Table II. The identity of chicks that abandoned their natal nests according to two measures of chick size

	Length of the 2nd primary (mm) $\bar{X} \pm SE$	Body mass (g) $\bar{X} \pm SE$
Abandoning chick	265.0 \pm 5.67	3305 \pm 45.82
Non-abandoning nestmates	212.0 \pm 6.98	3184 \pm 34.26
Wilcoxon <i>z</i>	3.2	1.98
<i>P</i>	<0.001	<0.05
Chick rank order		
1	91.0	63.0
2	9.0	32.0
3	0.0	4.5
4	0.0	0.0
χ^2 (<i>df</i> =3)	14.8	5.5
<i>P</i>	<0.01	NS

Mean values for abandoning chicks and their non-abandoning nestmates and percentages of the total number of abandoning chicks of known relative size according to their relative size rank are shown (rank 1=largest chick in its brood; $N=22$).

this prediction, we found a clear trend for those chicks that abandoned their natal nests to rank among the largest in their broods (Table II). It is unlikely that this is simply a result of chicks having to be capable of flight to switch nests because all their non-abandoning siblings were eventually capable of flying too, just a few days later.

A second possibility is that chicks abandoned their natal nests in response to increasing competition with siblings. During the last 3 weeks of the nestling period, white stork chicks become highly aggressive against any conspecific attempting to land on the nest, including siblings that practised flight exercises. In addition, parents provision nestlings at progressively lower rates during the last part of the nestling period (Tortosa & Redondo 1992b). Consequently, older chicks faced increasingly poorer conditions as they entered the phase of frequent flight exercise because they became more and more frequently attacked by their siblings on returning to their natal nests while, at the same time, parental feedings became more spaced in time. We tested this possibility by predicting that nest abandonment should occur at some age when it was no longer profitable for chicks to remain at their natal nests. This point roughly coincided with the time at which rates of sibling aggression exceeded 'per capita' feeding rates by parents (Fig. 2).

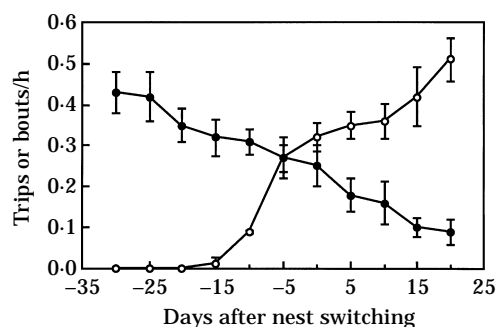


Figure 2. Changes in 'per capita' rates of food provisioning (feeding trips) by parents (\bullet , $N=11$) and aggression bouts against siblings attempting to land on the nest (\circ , $N=22$) in nests that were abandoned by chicks, plotted against the age at which abandonment took place. Values are $\bar{X} \pm SE$. Day 0 is the day of nest abandonment.

While it might sound appealing to interpret this point as a sort of threshold, or 'turning on' value in a cost/benefit-ratio function, we prefer, more parsimoniously, to regard it as casual. The key point is that chicks abandoned their nest when attacks from nestmates became frequent enough to exceed parental feedings per unit time, that is, when bouts of intensive activity at the nest began to consist mainly of aggression episodes. This in turn may explain why the eldest chicks (i.e. those exercising more often) in larger broods (i.e.

Table III. The occurrence of fostering across different brood sizes and the differential use of nests by adopted chicks according to brood size

	Brood size			
	1	2	3	4
Number of available broods	8	10	13	6
Number of fostering broods				
Observed	0	10	9	3
Expected*	4.7	5.9	7.7	3.6
Number of fostered chicks per brood ($\bar{X} \pm SE$)†	0.0 \pm 0.0	1.1 \pm 0.11	1.1 \pm 0.10	1.0 \pm 0.00

*Expected values were computed by assuming a random occurrence of fostering across different brood sizes; chi-squared: $\chi^2=19.3$, $df=3$, $P<0.001$.

†Only fostering broods; one-way ANOVA: $F_{1,18}=0.16$, NS.

containing more siblings) were the most likely to abandon their natal nests.

Costs of Nest Switching

Wandering chicks were never observed to be chased by adults in flight but they often elicited vigorous aggressive responses (pecking) by both resident adults and nestlings when attempting to land on a different nest. Typically, a wandering chick attempting to settle at a foster nest behaved in a characteristic way during the bouts of aggression by residents which immediately followed landing. It 'froze' crouching against the nest with the neck extended, a remarkable posture considering that most of the attacks were directed at the chick's head. A chick could remain immobile in this posture for as long as the residents kept on pecking at it (up to 30 min). Attacks became visibly more frequent and fiercer whenever the chick moved.

A successful adoption proceeded when an alien chick managed to resist the first bouts of aggression by residents and remained in the foster nest. Aggression rates against the strange chick steadily decreased over time and eventually approached standard values of aggression between relatives triggered by flight exercises (see below).

The probability of a chick being attacked when attempting to land on a strange nest varied according to the size of the resident brood. This could explain the observed frequency of adoptions across different brood sizes, which deviated from that expected by chance in relation to the availability of nests according to brood size (Table III).

The highest incidence of adoptions occurred in two-chick broods, where the probability of a wandering fledgling being attacked was lowest (see below). Broods containing singletons, which were very aggressive against approaching fledglings, were never observed to foster a strange chick, despite the fact that singletons enjoyed the highest feeding rates. Aggressive defence by residents was not, however, completely effective at driving off intruders. The percentage of landing attempts being contested by residents was similar for those broods that eventually adopted a strange chick ($\bar{X} \pm SE=51 \pm 6.0\%$, $N=12$) and for broods that never adopted (i.e. fed) any chick attempting to land ($63 \pm 5.3\%$, $N=20$; Mann-Whitney test: $Z=1.4$, NS).

Benefits of Nest Switching

Chicks moving into a foster nest could benefit in different ways. They could enjoy a longer period of parental care or higher feeding rates and lower aggression rates than at their natal nests, particularly if they managed to establish themselves in nests containing younger chicks (Pierotti & Murphy 1987).

Nest switching in this study, however, did not extend the period of parental care for adopted chicks. Considering only those chicks that were never observed to return to their natal nests after having been successfully adopted, the duration of parental care after adoption at the foster nests was significantly shorter ($\bar{X} \pm SE=5.5 \pm 0.29$ days) than the number of days that genetic parents continued to provision their siblings at their natal nests

Table IV. Changes in the number and age of nestmates and in the rates of parental provisioning and aggression by nestmates experienced by chicks that abandoned their natal nests and gained adoption at foster nests

	Natal nest $\bar{X} \pm SE$	Foster nest $\bar{X} \pm SE$	<i>N</i>	<i>P</i> *
Number of nestmates	2.16 \pm 0.17	1.70 \pm 0.14	24	<0.05
Brood age (days)	62.0 \pm 0.75	51.0 \pm 0.94	24	<0.001
Feeding rate (feedings/ chick per h)†	0.074 \pm 0.006	0.080 \pm 0.005	11	NS
Aggression rate (bouts/h)†	0.31 \pm 0.02	0.24 \pm 0.03	22	<0.05

*Wilcoxon test.

†Calculations refer to the 4 days before nest abandonment at natal nests and to the period of adoption at foster nests. In both natal and foster nests, abandoning chicks are included.

(14 \pm 0.56 days; Wilcoxon test: $z=2.1$, $N=18$, $P<0.05$).

Chicks that switched to foster nests also did not enjoy a feeding rate higher than that at their natal nests prior to adoption (Table IV). However, because of the progressive decrease in feeding rate that occurred at their natal nests by the time that nest abandonment took place (Fig. 2), adopted chicks were fed at the foster nests at slightly, but not significantly, higher rates ($\bar{X} \pm SE=0.080 \pm 0.05$ feedings/chick per h) than that they would have enjoyed at their natal nests if they had never abandoned them (0.057 ± 0.02 ; Wilcoxon test: $z=1.8$, $N=11$, $P=0.068$). This is, however, a very conservative estimate of the increase in food intake experienced by alien chicks as a consequence of adoption because it assumes that all nestlings (including the adoptee) received an equal share of the food regurgitated by parents on to the nest. In fact, alien chicks enjoyed a much more favourable position because of their larger size and probably consumed a large fraction of the incoming food. In particular, single large fish prey (e.g. carp, *Cyprinus carpio*) were repeatedly observed to be monopolized by alien chicks, which were better able to handle and swallow them than the younger resident chicks.

On the other hand, adopted chicks received less aggression from nestmates at the foster nests than at their natal nests, partly because they switched to nests containing both younger and smaller broods (Table IV). This suggests that chicks actually benefited from nest switching and that they gained a competitive advantage over their younger nestmates at the foster nests.

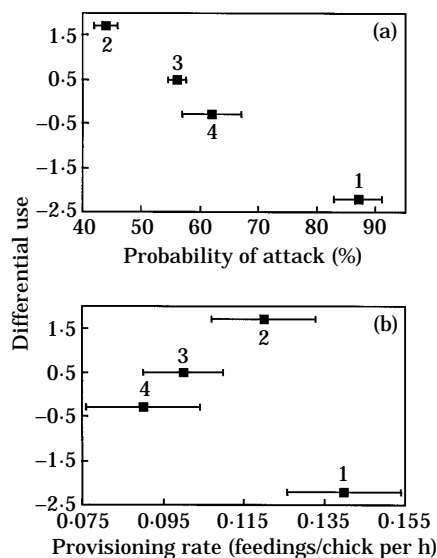


Figure 3. The differential use of broods of various sizes by chicks that gained adoption plotted against the probability of a landing attempt being aggressively contested by residents (a) and against the rate of food provisioning by foster parents (b). A differential use of zero indicates that fostering occurs in a proportion of broods that does not differ from that expected by chance. Positive values reflect a proportion higher than expected. Figures beside points indicate the size of the brood. Bars are SE around means.

Since both the food available to chicks and the risk of aggression by nestmates depended upon the size of the brood, it is worth asking whether

Table V. The effect of fostering a strange chick upon the duration of the period of food provisioning by adults and the change in body mass of resident chicks according to brood size ($\bar{X} \pm \text{SE}$)

	Brood size		
	2	3	4
Duration of the nestling period (days)*			
Fostering broods	90 ± 2.6	91 ± 1.6	104 ± 1.2
<i>N</i>	3	8	3
Non-fostering broods	89 ± 2.1	92 ± 2.3	108 ± 3.9
<i>N</i>	3	10	3
Mass increment (% of body mass)†			
Pre-fostering period (40–50 days)			
Fostering broods	14.30 ± 2.89	11.70 ± 1.65	7.60 ± 2.49
<i>N</i>	5	15	7
Non-fostering broods	7.20 ± 2.69	10.00 ± 1.30	9.32 ± 3.37
<i>N</i>	6	25	3
Mass increment (% of body mass)‡			
Fostering period (50–60 days)			
Fostering broods	0.275 ± 0.39	− 5.30 ± 1.40	− 4.71 ± 1.00
Non-fostering broods	0.887 ± 0.34	− 2.15 ± 1.19	− 2.24 ± 3.07

*Two-way ANOVA: $F_{2,29}(\text{brood size})=8.1$, $P<0.01$; $F_{1,29}(\text{fostering})=0.05$, NS; $F_{2,29}(\text{brood size} \times \text{fostering})=0.39$, NS.

†Two-way analysis of covariance with two covariates (hatching order: $F_{1,56}=1.7$, NS; chick age: $F_{1,54}=4.6$, $P<0.04$): $F_{2,56}(\text{brood size})=0.6$, NS; $F_{1,56}(\text{fostering})=1.3$, NS.

‡Two-way analysis of covariance with two covariates (hatching order: $F_{1,56}=11.6$, $P<0.01$; chick age: $F_{1,54}=3.95$, $P=0.05$): $F_{2,56}(\text{brood size})=1.85$, NS; $F_{1,56}(\text{fostering})=5.89$, $P<0.025$.

differences in these two variables explained the differential use of nests according to brood size. Aggression by residents was the best predictor of the extent of fostering across different brood sizes (Fig. 3). A composite predictor calculated as the ratio between both independent variables (i.e. 'feedings/chick per h per landing attempt that was aggressively contested') is biologically meaningless, and anyway failed to explain differential use better than aggression alone.

Costs of Fostering

No chick mortality occurred as a consequence of fostering. Foster parents showed only a weak, non-significant trend to adjust feeding rates to the increase in the number of chicks (2 days before adoption, $\bar{X} \pm \text{SE}=0.28 \pm 0.013$ feedings/h; during adoption, 0.31 ± 0.020 feedings/h; paired $t=1.95$, $df=12$, $P=0.07$); but, as a consequence, 'per capita' feeding rates for resident chicks decreased after adoption of the alien chick took place

(before: 0.1 ± 0.006 feedings/chick per h; after: 0.079 ± 0.005 ; Wilcoxon test: $z=3.1$, $N=13$, $P<0.01$). This had a measurable negative effect upon the growth of resident chicks during the period of adoption. On average, chicks in broods containing an alien young showed half the relative mass increment as that of chicks of similar characteristics in non-fostering broods (Table V).

Adopting a strange chick had no apparent effect upon the duration of the nestling period at fostering nests, which did not differ from that of broods of comparable size that did not foster any fledgling (Table V).

Benefits of Fostering

Adults caring for their own broods clearly gained no future benefits from the experience of chick-rearing by accepting an extra chick. This is stressed by the fact that no adoption took place in single-chick broods (where parents could perhaps

Table VI. The probability ($\bar{X} \pm \text{SE}$) that resident adults and chicks in broods of different sizes responded aggressively to a landing attempt by an alien or resident chick expressed as a percentage of the total number of landing attempts per nest

	Brood size				Total
	1	2	3	4	
Colonial nests (<i>N</i>)	4	9	18	6	
Adults*					
Alien chick	50.0 ± 13.3	26.0 ± 2.6	40.0 ± 1.2	31.0 ± 6.7	36.0 ± 0.8
Own chick	0.0 ± 0.0	0.0 ± 0.0	3.5 ± 0.3	16.0 ± 0.7	2.0 ± 0.1
Chicks†					
Alien chick	100.0 ± 0.0	45.0 ± 2.8	64.0 ± 1.7	75.0 ± 3.1	65.0 ± 0.7
Sibling	—	14.6 ± 1.2	26.5 ± 0.6	35.2 ± 0.9	24.0 ± 2.7
Total					
Alien chick	87.0 ± 4.0	44.0 ± 2.1	56.0 ± 1.0	62.0 ± 4.9	57.0 ± 0.6
Resident chick	—	9.0 ± 0.6	15.0 ± 0.5	21.0 ± 0.9	14.4 ± 0.2
Solitary nests (<i>N</i>)	0	1	6	1	
Total against resident chicks‡		11.5	10.4 ± 2.1	17	11.3 ± 1.8

*Two-way ANOVA: $F_{3,84}(\text{brood size})=57.9$, $P<0.001$; $F_{1,84}(\text{alien versus own})=3.0$, $P<0.05$; $F_{3,84}(\text{alien versus own} \times \text{brood size})=2.9$, $P<0.05$.

†Two-way ANOVA: $F_{2,76}(\text{brood size})=61.7$, $P<0.001$; $F_{1,76}(\text{alien versus sib})=4.4$, $P<0.01$; $F_{2,76}(\text{alien versus sib} \times \text{brood size})=0.1$, NS.

‡Student's *t* (brood size=3), $t=2.1$, $df=22$, $P=0.05$.

gain experience in rearing a multiple brood). Also, it seems unlikely that adoption would lower the risk of the adopters' chicks being preyed upon, since predation on old chicks is virtually non-existent.

It is also unlikely that fostering is a kin-selected trait. Although the degree of relatedness for most birds involved in nest switching was unknown, there is some evidence for differential natal philopatry according to sex which does not support this possibility. Our data indicate that 60% of males (12/20) and 38% of females (5/13) returned to breed at their natal colony (chi-squared test, $\chi^2=1.46$, $df=1$, NS). Dispersal distances for juvenile males were also shorter ($\bar{X} \pm \text{SE}=18.3 \pm 1.1$ km, $N=21$) than for juvenile females (35.0 ± 4.0 km, $N=13$; $t=1.45$, $df=35$, $P<0.05$). Males do not only show stronger natal philopatry than females but also tend to breed closer to parents and siblings when returning to their natal colony (F. S. Tortosa, unpublished data). Overall natal philopatry seems too low to allow a high probability of fostering chicks of close relatives, and any kin-selected trait would be more likely to be expressed in males. However, females and males seemed to be equally unwilling to accept a strange chick. When both members of a pair were present at the nest during a landing attempt by a

wandering chick ($N=29$) males attacked first in 52% (± 6.0 SE) of cases and females in 48% (± 6.0 ; Wilcoxon test: $z=0.53$, NS). In addition, females were not more reluctant to regurgitate food than males when the brood contained an alien chick. The time elapsed between arrival at the nest by a parent and effective regurgitation of food was 51 s (± 18 SE) for males and 55 s (± 21) for females (Wilcoxon test: $z=0.72$, $N=20$, NS). However, contrary to expectations, by the time adoptions were more likely to take place (50–90 days), females contributed a significantly higher proportion of feedings ($\bar{X} \pm \text{SE}=58.2 \pm 8.0\%$) than did males ($41.8 \pm 8.0\%$; Wilcoxon test: $z=3.16$, $N=23$, $P<0.001$). Such a sex difference probably simply reflects that females are caring more nearer the end of the nestling period for some other reason, rather than an effect related to adoptions.

No evidence of reciprocity between years (Pierotti 1980) or within a given breeding season could be found in this study. None of the cases of nest switching observed involved the interchange of chicks between the same two nests. This is of course what we should expect if nest switching involved almost fledged chicks moving into younger broods. Hatching dates of nests that were abandoned were earlier ($\bar{X} \pm \text{SE}=9 \pm 1.4$ days after hatching of the first brood in the colony, $N=24$) than those of nests

that eventually adopted a chick (19 ± 1.8 days, $N=20$; Mann-Whitney test: $z=2.1$, $P<0.05$).

Discrimination against Non-kin?

Both resident adults and chicks directed a significantly higher proportion of attacks towards a strange chick than towards a familiar chick attempting to land on the nest (Table VI). Chicks were far more aggressive towards alien chicks than adults (Wilcoxon test: $z=3.8$, $N=33$, $P<0.001$). When both adults and chicks were present during landing attempts by a strange chick, resident nestlings accounted for a larger proportion of attacks ($\bar{X} \pm SE = 68.5 \pm 5.3\%$) than adults ($31.5 \pm 5.3\%$; Wilcoxon test: $z=4.48$, $N=37$, $P<0.001$). However, once they managed to establish themselves at foster nests, alien chicks experienced decreasing levels of aggression by residents. In fact, a day-by-day analysis of aggressive discrimination against strange chicks during the period of adoption revealed that the observed difference in probabilities of aggression towards resident versus alien chicks was restricted to the day on which adoption took place. On that day, the probability of a flying movement by an alien chick being aggressively contested was 40.4% (± 3.3 SE) while the comparative figure for a resident chick was 25.2% (± 3.1 ; Wilcoxon test: $z=2.7$, $N=16$, $P<0.05$). In contrast, on the following days the probability of a chick being attacked when landing on the nest was similar for alien ($33.1 \pm 2.8\%$) and for resident chicks ($28.5 \pm 3.9\%$; Wilcoxon test: $z=1.3$, $N=16$, NS). This suggests that residents did not actually recognize their kin but were capable of some discrimination against unfamiliar chicks.

Such a discrimination rule is obviously open to errors, particularly when chicks fly to and from their natal nests during the last part of the nestling period. That aggression between siblings (or parents and chicks) was a product of discrimination errors and not the result of any strategy promoting the independence of eldest chicks is suggested by several lines of evidence. First, aggression against kin was more common in colonial than in solitary nests (Table VI), which suggests that aggression was a response to wandering rather than to resident chicks. Second, we should expect that the probability of attacking kin that are not individually recognized would increase with brood size (simply because the chances of encountering

siblings increase with the number of chicks in the brood). In fact, parents caring for singletons or two-chick broods were never observed to misdirect an attack, and the percentage of aggressions received by resident chicks increased with brood size (Table VI). In addition, nests containing singletons showed the highest probability of displaying an aggressive response against alien chicks, despite the fact that we would expect this probability to increase with brood size simply because of an increase in the number of defending birds (Table VI), which might imply that individual chicks in larger broods were less aggressive. This makes sense if aggression between siblings is in fact a cost of a defensive system that fails to recognize chicks individually. Apart from attacking alien chicks more frequently during the initial phases of adoption, foster parents apparently did not behave differently when an alien chick was present in their broods. The time elapsed since a parent arrived at the nest with food until regurgitation was similar for nests containing an adopted chick ($\bar{X} \pm SE = 49.0 \pm 3.3$ s, $N=20$) and for nests of a comparable age containing no strange chicks (41.0 ± 3.5 s, $N=15$; Mann-Whitney test: $z=1.05$, NS)

DISCUSSION

Nest switching affected approximately 40% of white stork broods at three breeding colonies. Adopted chicks seemed to benefit by reaching nutritional independence in foster broods in which they enjoyed both lower aggression and a more favourable feeding position than in their natal broods. These facts suggest that alloparental care in this species is not a maladaptive consequence of accidental reproductive errors or human disturbance (Holley 1981; Pierotti 1988). Apparently, the effect of fostering an alien chick for residents was weak. Foster parents did not gain any direct benefit from adopting a strange chick, such as reproductive experience or dilution of predation risk for their own brood. Also, as in other species studied (e.g. gulls) there was no evidence of residents gaining any benefit through kin selection or reciprocal altruism (Holley 1981; Waltz 1981; Pierotti 1982, 1991; Hebert 1988). On the other hand, adoptions took place at a slight cost for resident adults and chicks. Foster parents did not extend the period of food provisioning, and only

slightly increased feeding rates to accommodate the extra chick. As a consequence, resident chicks experienced decreased feeding rates during the period of adoption and this had a measurable negative effect upon their mass gain. It is unclear, however, whether the 2% lower mass gain of chicks in fostering broods had any subsequent effect upon their survival. In any case, adoptions caused no chick mortality prior to fledging. This result contrasts with findings from previous studies in gulls and terns in which adopting an alien chick severely affected the number or quality of resident chicks (Carter & Spear 1986; Pierotti & Murphy 1987; Morris et al. 1991). Unlike for seabirds, adoptions in white storks took place late in the nestling period, when resident chicks had almost completed growth, and thus lasted for a few days. Therefore, they had a much more benign effect upon the food intake of resident chicks than in semi-precocial seabirds, in which adoptions often impair the growth of very young chicks.

Many of our results fit well with the predictions of the 'inter-generational arms race' model (Pierotti & Murphy 1987; Hebert 1988) but it is worth making some clarifications.

(1) There was an asymmetry in current selection pressures for chicks seeking adoption and fostering adults, because adoption directly benefited chicks at a very slight cost for residents. Accordingly, chicks were equipped with appropriate behavioural mechanisms (some sort of tonic immobility) that counteracted the aggressive defence by residents.

(2) Chicks that abandoned their natal broods were those that benefited more from becoming adopted. In semi-precocial gulls and terns, this affects mainly chicks with low chances of survival, in particular late-hatched chicks in asynchronous broods or chicks receiving substandard parental care at their natal nests (Graves & Whiten 1980; Pierotti & Murphy 1987; cf. Morris et al. 1991). Altricial chicks, in contrast, can switch nests only near fledging which, by definition, means that they have received an adequate amount of care. Incidentally, this implies weaker selection for becoming adopted in altricial than semi-precocial young (Pierotti 1988).

Nest switching among altricial birds has been documented in cattle egrets, *Bubulcus ibis* (Blaker 1969), herons, *Ardea cinerea* (Milstein

et al. 1970), both colonial (kites, *Milvus* spp.: Bustamante & Hiraldo 1990; lesser kestrel, *Falco naumanni*: Donazar et al. 1991) and solitary (ospreys, *Pandion haliaetus*: Poole 1982; Egyptian vultures, *Neophron percnopterus*: Donazar & Ceballos 1991) raptors, and white storks in this study. Many of these species show special flight adaptations, either because of their large size (e.g. herons, ospreys, vultures and storks) or specialized foraging tactics (e.g. raptors). Hence, they may require maturation of complex motor patterns for a sufficiently long period prior to fledging. The 'flying nestlings' of these species are particularly suited to kleptoparasitize other broods, especially when nests are close to each other. When a lengthy training period is more costly to perform at old than at younger broods (because older chicks are provisioned less, attacked more frequently by siblings, or both), chicks would benefit from switching to a younger brood where competition is milder. If, as in storks, these costs increase with increasing brood size, it follows that chicks that benefit more from adoption will be those in a more advanced stage of development. Compared with their younger nestmates, these senior chicks have, by definition, higher exercising requirements and lower expectations of spending their training period in a smaller ($N-1$) natal brood, as well as the highest number of potentially suitable foster broods available in the colony.

(3) Chicks seeking adoption should attempt to move into younger broods in order to gain a competitive advantage. This proved true for white storks, as well as other species (Poole 1982; Pierotti & Murphy 1987; Hebert 1988; Bustamante & Hiraldo 1990; Morris et al. 1991). However, it is unclear whether this pattern is the result of chicks trying to optimize their destination or, more parsimoniously, is a by-product of younger broods being less aggressive against intrusions (Holley 1988). In the case of white storks, aggression by residents alone was the best predictor of the extent of fostering across different brood sizes.

(4) Adopting a strange chick should be costly to foster parents and, consequently, they should discriminate against unrelated chicks. As a corollary of this prediction, adults are expected to be less willing to accept a strange chick when the cost of adoption is high (Pierotti & Murphy 1987). Like other species of colonial breeders in

which parents stand a risk of adoption, white storks were able to reject unrelated young (mammals: Riedman & Le Boeuf 1982; Blaustein et al. 1987; Gustin & McCracken 1987; birds: review in Redondo 1993). Aggressive discrimination was, however, mild enough to allow frequent adoptions to occur. As discussed above, adoptions should be more costly, and discrimination more effective, in species with early-mobile young, for example, most colonial seabirds in which rejection of intruders often results in fatal attacks by residents (Pierotti 1988). Killing of alien chicks has also been reported in cattle egrets (Blaker 1969) but not in grey herons (Milstein et al. 1970). Unlike grey heron and white stork, cattle egret chicks become highly mobile early in life, scrambling around the nesting trees as soon as they cease to be brooded by parents (Blaker 1969).

These considerations suggest that fostering behaviour in white storks may be the result of an inter-generational arms race with weak selection pressures for both parties. However, this poses two seemingly paradoxical questions as follows. First, if costs of fostering are so low, why have residents evolved discrimination responses against alien chicks at all? A likely solution for this question, consistent with the arms-race concept, is that current costs to fosterers are low precisely because of the existence of a defensive mechanism. Our results show that intensity of defence by residents determines the extent of adoption across different brood sizes, suggesting that defence is effective at driving off intruders. It is possible that actual levels of defence are efficient enough to guarantee that only one intruder is adopted at a time, which in turn ensures that resident chicks do not experience a substantial decrease in food intake. In other words, defence may prevent multiple adoptions occurring simultaneously, a situation that is potentially more costly. Second, provided that defence is effective at deterring wandering chicks, why has not a more refined, totally efficient system of defence evolved? In the case of white storks, kin discrimination appears to be good enough for visits by alien chicks not to extract a significant cost (see also Beecher et al. 1981) but this is obviously not the case for species in which adoption is costly.

Unlike insects and mammals, which are capable of recognizing kin individually through efficient (e.g. phenotype-matching) mechanisms based on

olfactory clues, birds may be constrained to rely on visual and acoustic traits to recognize their offspring (Beecher 1988; Davies et al. 1992). Information-rich signature traits may be difficult to evolve if chicks are selected to conceal their identity, as in brood parasites (Beecher 1989). Since most visual and acoustic features often change dramatically during development, this may have prevented the evolution of completely efficient systems of chick discrimination because of the existence of associated costs in the form of time loss (which may affect the efficiency of foraging; Beecher et al. 1981) and risk of making irreversible mistakes by rejecting own chicks (Knudsen & Evans 1986; Davies & Brooke 1988; Hebert 1988). Given a low probability of adopting a strange chick, and/or a low cost of adoption, this may select for a more general mechanism of kin discrimination in which the average cost of misfeeding is less than the cost of evicting a resident chick (Beecher et al. 1981; Pierotti & Murphy 1987). Consistent with this possibility, more precise recognition of individual offspring has apparently evolved in truly colonial, semi-precocial birds such as murrets and terns in which both the potential for nest switching is high (unlike gulls, which nest as far apart as conditions allow) and the cost of adoption is high (unlike altricial species; Pierotti & Murphy 1987). A general mechanism of discrimination is, however, open to exploitation by parasites and the cost of adoption may ultimately determine the effectiveness of the defensive system and vice versa (Redondo 1993).

This study suggests that an arms race between parasites and their hosts may end in an evolutionary equilibrium maintained by the existence of costs associated with highly effective mechanisms of discrimination (Lotem et al. 1992; Lotem 1993). Defensive strategies by hosts may reach a level of effectiveness sufficient for parasitism to exert an almost neutral effect upon the reproductive success of hosts. Beyond this point, there is no longer selection for further improving the defensive mechanism, which may allow parasites to co-exist with hosts over time.

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