

Brood reduction in the American white pelican (*Pelecanus erythrorhynchos*)

Kevin J. Cash and Roger M. Evans

Department of Zoology, University of Manitoba, Winnipeg, Manitoba, Canada, R3T 2N2

Received April 17, 1985 / Accepted October 22, 1985

Summary. American white pelicans (*Pelecanus erythrorhynchos*) breeding in colonies at East Shoal Lake, Manitoba, Canada exhibited a mean hatching asynchrony of 2.5 days in 2-egg clutches. This resulted in a size difference between chicks which facilitated sibling dominance, harassment and lack of food for the subordinate chick. Only one young survived per nest. In marked broods, the second-hatched chick survived in 20% of successful nests. Manipulated clutch sizes (1, 2 and 3 eggs or chicks per nest) revealed that the presence of a second chick contributes significantly to the reproductive success of the parents. Results support the hypothesis that the second egg functions as a form of “insurance” against early loss of the first egg or chick. The parents, by establishing hatching asynchrony, by nonintervention in sibling aggression, and by selectively feeding the dominant chick, maximize their chance of rearing the most viable young.

Introduction

The major hypothesis concerning the adaptive significance of brood reduction in birds, originally proposed by Lack (1947), suggests that females of many species produce clutches of greater size than typical food conditions allow them to rear to fledging. Lack further proposed that brood size is reduced to meet prevailing food conditions, reduction being facilitated by asynchronous hatching resulting in different-sized nestlings with different competitive abilities. The younger, smaller nestlings may then be eliminated, usually by starvation, in times of food stress (Lack 1947, 1954, 1958). Many studies in brood reduction have since

demonstrated that competitive gradients exist within the broods of a variety of species (Nisbet and Cohen 1975; Parsons 1975; Howe 1976, 1978; O'Connor 1978; Bengtsson and Ryden 1981; Hahn 1981; Braun and Hunt 1983; see also Mock 1984 for a review). In most cases the last-hatched chick is significantly smaller than its siblings and perishes when food is scarce (Lack 1954, 1968; Mock 1984).

A special case of brood reduction theory, termed the “insurance-egg” hypothesis, was first proposed by Dorward (1962) to explain the evolution of clutch size in white (*Sula dactylatra*) and brown (*S. leucogaster*) boobies. In these species, two eggs are typically laid but both young “rarely” fledge. The insurance-egg hypothesis holds that despite a failure to rear two young, the second egg is produced because it insures against loss or infertility of the first egg or early death of the first chick. Should the older sibling die then the second can be raised. If the first is healthy, then the younger chick is eliminated, usually through sibling aggression, thereby achieving a brood size that can be fed successfully and raised to maturity. This hypothesis has yet to be examined in detail for any species (Mock 1984). The purpose of this study was to examine the insurance-egg hypothesis and the brood reduction that is implicit in this hypothesis, in the American white pelican (*Pelecanus erythrorhynchos*).

This synchronously nesting colonial species breeds in large numbers and both chicks from the usual two-egg clutch survive in fewer than 10% of the nests (Knopf 1979; Bunnell et al. 1981). Sibling harassment leading to the death of one chick by starvation or exposure is the mechanism by which the brood is reduced (Schaller 1964; Knopf 1979).

Methods

We studied white pelicans breeding on colonies at East Shoal Lake, Manitoba, Canada (see O'Malley and Evans 1980 for description) in the summers of 1982 and 1983. Two hundred and fifty six nests were counted on the study colony in 1982, and 655 nests at a different colony studied in 1983. Colony occupation was observed from a distance of approximately 2 km to determine the onset of breeding for each year (Evans and Cash, in press). About six days prior to the expected hatch date a blind was erected at the edge of the study colony, at least 5 m from the nearest nest. The blind was entered through a 40 m, above ground plastic tunnel (Shugart et al. 1981) in 1982 and approached through a shorter (8 m) tunnel and floating blind (Nuechterlein 1980) system in 1983.

Behavioural observations

Observations of nests began 2 to 3 days prior to hatch initiation and continued daily until creches formed (Evans 1984) when the young were about 20 days old. In 1982, 114 h of observations were made at 13 individually identifiable nests from 1 to 22 June while in 1983, 98.5 h of observations were made at 32 nests from 1 to 24 June.

Data collected for each nest were: (1) the time between hatching of the first and second chicks, (2) feeding frequency, (3) when visible, prey size, as estimated from adult bill length, (4) recipient of food (larger or smaller chick), (5) whether the larger or smaller chick was toward the front or rear of the brooding adult, (6) nature, context and duration of aggressive encounters between chicks, (7) parental response, if any, to chick aggressive encounters and (8) the timing of brood reduction relative to when the second young hatched. In all analyses for which no significant differences occurred between years, the data have been lumped.

Brood reduction and survival of marked broods

In 1983, two nesting areas approximately 50 m from the observation nests were selected for experimental manipulation. On 3 June the first-hatched chick in each of 50 nests was marked on the ventral surface with a nontoxic permanent felt marker. In most cases the second egg was pipped when the older chick was marked. Where both chicks hatched the older sibling was readily distinguished because it was larger and lighter in colour. These broods were then censused, by walking through the nesting area, every two days from 3 to 15 June, when young had become too mobile to associate them with individual nests.

Egg and brood success at manipulated nests

On 19 May 1983, approximately 13 days before hatching began, we manipulated 60 2-egg clutches to produce 20 matched triads of nests, each triad containing one clutch each of 1, 2 and 3 eggs. The triads minimized any biases associated with the location of the nests in the colony (Burger 1974; McCrimmon 1980). As there is no evidence of a difference in hatching success between first and second laid eggs (O'Malley and Evans 1980), we did not distinguish between them. Because adjacent nests of pelicans are highly synchronized (Knopf 1979) we assumed that the egg added to nests to produce 3-egg clutches did not differ markedly in its laying date. Observed hatching intervals validated this assumption.

Triads were censused every two days from the beginning of hatch (1 June), until the initial stages of creche formation (21 June), when chicks could no longer be associated with specific nests. Three nests which failed to hatch a complete clutch were adjusted by adding one chick of appropriate size and age

from adjacent nonexperimental nests. Complete loss of 3 triads (9 nests) reduced the sample size to 17 triads (51 broods) during the nestling stage.

Previously published reports (Schaller 1964; Johnson and Sloan 1978; Knopf 1979; Bunnell et al. 1981) indicated that white pelicans rarely raise more than one young to the creche stage. A nest was therefore considered to be "successful" if at least one egg hatched. Similarly, a brood was considered "successful" if at least one young survived to the creche stage. As mortality in the creche is low (1%, Knopf 1976), any chick which survived to the creche stage was likely to fledge.

Results

Behavioural observations

Hatching in the study colony began in both years on 3 June and was completed by 11 June. The degree of hatching asynchrony within nests did not differ significantly between years ($t=0.27$, $P>0.05$) and averaged 2.5 ± 1.1 (SD) days ($n=45$).

Following hatch of the second egg the relative position of each chick in a particular nest was noted at the beginning of each observation period. In 60 of 62 cases (96.8%) in which both chicks could be identified, the larger chick occupied a position under the anterior breast feathers of the adult while the smaller chick remained behind its sibling.

At this stage, adults fed the young by regurgitating small pieces (<10 cm long) of partially digested fish into the pouch. The young then fed from the tip of the parent's lower mandible. Only twice (3.6% of 55 observed feeds) did adults deliver items too large to be manipulated by chicks. On each of these occasions the adult swallowed the fish.

From its more anterior position, the larger young had better access to food offered by the parent. Larger chicks were never observed to beg without gaining access to the parent's pouch. Of 36 feedings observed at nests with two young, 32 (88.9%) were directed only toward the older chick. Of the remaining four feedings, two involved both chicks feeding simultaneously. The larger chick was higher in the mandible during these two feedings and so may have received most of the food. In only two instances (5.5% of the feedings) was the younger chick fed exclusively. The few feedings directed toward the smaller sibling correlates with its slower rate of growth, as estimated by eye, in most of the nests. Slow growth was also characteristic of the smaller young in most other nests observed away from the main observation area during this period.

Adults normally made no obvious attempts to feed the more posteriorly positioned chick. On sev-

eral occasions they ignored its intense begging. Two instances were observed of a dominant chick not preventing the smaller young from moving into the anterior position, and these were also the only times we saw the smaller chick fed exclusively.

Context and description of harassment of siblings

Sibling harassment was noted in 17 of 18 (94.4%) instances when the brooding parent rose to stretch or preen. If aggression occurred while the young were being brooded we were unable to detect it. When the parent stood up, both young were typically in the forward half of the nest. The larger chick then pecked its sibling about the back or head, or grasped the smaller bird by the neck, forcing it toward the rear of the nest. What appeared to be blood or bruises were often noted on the head and back of the smaller chick. This was later verified when chicks were examined in other parts of the colony. The duration of aggressive bouts between siblings ranged from 34 to 300 s ($\bar{x}=127$, $n=17$). Aggression typically terminated when the smaller chick retreated toward the rear of the nest or the adult resumed brooding. Only twice did parents intervene to prevent sibling aggression; on both occasions the parents in question were attempting to resume brooding.

Continued sibling harassment and a lack of food delivered to the smaller young contributed to a growing disparity in chick size, until the smaller bird perished. Given that the second chick was seldom fed and hence grew little, its death was probably due to starvation. However, live though greatly weakened chicks observed outside the nest cup in other parts of the colony indicate that death by exposure may also occur.

In 1982 the mean period between hatch of the second young and the occurrence of brood reduction was 3.7 ± 2.4 days ($n=13$ nests). The time until chick death in 1983 was 4.9 ± 2.8 days ($n=32$ nests), slightly but significantly longer than in 1982 ($t=1.793$, $P<0.05$).

Brood reduction and survival of marked broods

Survival of marked broods at 12 ± 1 days of age is given in Table 1. Forty-five (90%) of the 50 marked broods contained a single chick at this time. In four of the five nests that failed, both chicks disappeared during the 12-day period. The possibility of chick loss to gulls following a census but prior to the return of adult pelicans to the nest cannot be totally ruled out. Our observations of both pelicans and gulls as we left the area suggested however, that the brooding adults normally

Table 1. Status of 50 broods late in the nestling period (12 ± 1 days of age)

Brood status	<i>n</i>	%
Younger chick missing or dead, older present	36	72
Older chick missing or dead, younger present	9	18
Both chicks missing or dead	5	10
Both chicks present	0	0
Total	50	100

Table 2. Hatching success of manipulated clutches and chick survival (18 ± 3 days old) in manipulated broods

Situation	Clutch size		
	1	2	3
No of clutches that hatched			
0 eggs	3	3	3
1 egg	17	1	0
2 eggs	—	16	2
3 eggs	—	—	15
Total	20	20	20
No. of eggs hatched (%)	17(85.0)	33(82.5)	49(81.7)
No. of successful ^a nests (%)	17(85.0)	17(85.0)	17(85.0)
No. of surviving young/brood	0.4	0.7	0.6
No. of successful ^b broods (%)	8(47.1)	15(88.2)	12(70.6)

^a Success is the hatching of at least one egg per nest

^b Success is defined as the survival to creche stage of at least one chick per brood. None of the nests contained more than one young at that time (see text)

had returned to the nest before the young could be preyed upon.

At the end of the census period (15 June), when each successful nest contained only one young, 20% of the surviving young were from second-hatched eggs. There was no significant difference in the timing of brood reduction (the period from the hatch of the second chick to the death of one young) involving loss of the older, as opposed to younger, chick (median test, $P<0.05$).

Egg and brood success at manipulated nests

The proportion of eggs which hatched successfully in each nest did not vary significantly with manipulated clutch size ($\chi^2=0.151$, $P>0.05$, Table 2). At least one egg hatched in 17 (85.0%) of the nests of each clutch size. At the end of the census period for manipulated broods (21 June), when young were 18 ± 3 days old, 34 (97.1%) of the 35 surviving broods consisted of a single young. One brood, of two young (originally a three-chick brood), contained a weakened and immobile chick. It is unlike-

ly that this chick would have survived to enter the creche, thus the brood in question was recorded as containing a single chick at the time of creche formation.

The manipulation of broods revealed that the number of successful broods (Table 2) differed significantly with brood size ($\chi^2=6.74$, $P<0.02$, for all broods combined). Success of broods which originally contained one vs. two chicks (47.1% vs 88.2%) differed significantly ($\chi^2=6.58$, $P<0.02$). Broods of three, with a success rate of 70.6% were intermediate and did not differ significantly from broods of one ($\chi^2=1.94$, $P>0.05$) or two ($\chi^2=1.62$, $P>0.05$). Excluding the one 2-egg clutch which was adjusted at hatching, 14 (73.7%) of the remaining 19 2-egg clutches reared a young to the creche stage, but only 8 (40.0%) of 20 1-egg clutches did so. Therefore overall success differed significantly ($\chi^2=4.48$, $P<0.05$) between 1- and 2-egg clutches. Parents of 2-egg clutches, on average reared 0.7 chicks to the creche stage while pairs having 1-egg clutches reared on average of 0.4 chicks to the creche stage (Table 2).

Discussion

This study appears to be the first direct test of the insurance-egg hypothesis (Mock 1984), as well as the first detailed examination of sibling aggression and brood reduction in pelicans. Results of the marking experiment indicate that, contrary to other reports (Schaller 1964; Cooper 1980), the second chick does sometimes survive (20% of the cases, $n=45$) when the first does not. Furthermore, as shown by experimental manipulation of broods, the presence of a second chick at hatching made a significant contribution to the parent's eventual reproductive success, despite the low probability (essentially zero in this study) of rearing more than one chick to the creche stage. Results of this study thus clearly support the insurance-egg hypothesis for white pelicans. The high hatching success of first laid eggs (Table 2) as well as the moderate mortality rates among first-hatched chicks (Table 1) and the high mortality rates of chicks in broods of one (Table 2) indicate that the second egg acts primarily as insurance against loss of the first chick rather than insurance against infertility or loss of the first egg.

The young were still relatively small when brood reduction occurred as were food demands placed on parents, who appeared capable of delivering sufficient amounts of food to the chicks.

There was therefore no evidence to suggest that brood reduction was an immediate consequence of the inability of parents to deliver enough food to the young at the time brood reduction occurred. However, as pointed out by Mock (1984), siblicide may be an evolutionary response on the part of the dominant chick to "anticipated" food shortages that might occur later in development when the larger young require substantially more food. Under such circumstances the dominant chick would presumably benefit by eliminating its sibling as soon as possible. If so, brood reduction in white pelicans may be indirectly food-related, despite the seeming abundance of food that the parents are capable of providing at the time brood reduction occurs. To our knowledge food limitation in American white pelicans at any stage has not been examined.

As mentioned earlier the insurance-egg hypothesis (Dorward 1962) and Lack's (1947) original food-related hypothesis of brood reduction are not mutually exclusive and may act together in the evolution of larger clutch size (Nisbet 1975; Nisbet and Cohen 1975). The second egg or chick may act as insurance during the early nestling period while thereafter the probability of both chicks surviving could depend on food availability in that particular year. The fact that some studies (e.g., Knopf 1979) reported that both chicks survived in up to 10% of white pelican nests is consistent with this interpretation. Studies (Schaller 1964; Johnson and Sloan 1978; Sloan 1982) which found white pelican productivity to be less than one chick per nest and the high mortality rates (28.0% to 52.9%) among first-hatched young in this study suggest however, that selection favouring the existence of an insurance egg is the most direct explanation for the evolution of a two-egg clutch in white pelicans.

The role of the parent in brood reduction is an important, though superficially passive one, and requires some explanation. O'Connor (1978), using kin-selection (Hamilton 1964) and parent-offspring conflict (Trivers 1974) theories, has constructed a model of fratricide (siblicide), infanticide and suicide. The model allowed O'Connor to predict that sibling rivalry and aggression should be great in small broods. Our results agree with this prediction.

O'Connor (1978) also predicted that conflict between a parent and potential survivor offspring would be most intense in small broods, and that such conflict would manifest itself most readily in parental intervention to prevent sibling aggression.

These predictions seem consistent with kin-selection and parent-offspring conflict theories, yet we found that parents did not intervene to prevent sibling aggression. Nor has such intervention been noted in pink-backed pelicans (*P. rufescens*) (Din and Eltringham 1974), Australian pelicans (*P. conspicillatus*) (Vestjens 1977), or in several species of African eagles (Meyburg 1974). We suggest this apparent contradiction rests with O'Connor's assumption that brood reduction is always a response to prevailing food conditions, despite his recognition of the role of an insurance-egg in some species.

Parent-offspring conflict, according to O'Connor's model, arise because at some point during the nesting cycle the parent is selected to invest equally in each chick provided the probability of rearing both is sufficiently high. The potential survivor however, presumably benefits from more investment than the parent is selected to provide. If food supplies deteriorate, the probability of rearing both chicks falls sufficiently such that at a certain point the parent's best strategy becomes one of directing all investment toward one chick and allowing the second to perish. At this point conflict between the adult and potential survivor ends. Our results suggest that this point of nonconflict between and potential survivor was the norm in the colony studied.

When only one chick can normally be reared by the parents they should benefit most by rearing the more viable young. The slight but significantly larger size of first-hatched eggs in this species (O'Malley and Evans 1980) would be expected to enhance the relative viability of the older young. Asynchronous hatching and the resulting size differential may provide a mechanism by which parents can increase their chances of raising the most viable young. Should the first chick be less than adequately viable, however, the second young would still be able to overcome its size disadvantage and become dominant over its sibling. The parents, by not interfering in aggression and by feeding only that chick in the dominant position, permit reversals of status based on the competitive abilities of the young and therefore ensure that the most viable offspring survives.

Acknowledgements. We would like to thank, R.M.R. Barclay, R.A. Brust, H.R. Carter, P.N. Hebert, S.G. Sealy and two anonymous reviewers for their valuable comments on earlier drafts of this manuscript. This study was supported by grants to Evans from the Natural Sciences and Engineering Research Council of Canada and the Wildlife Branch, Manitoba Department of Natural Resources.

References

- Bengtsson H, Ryden O (1981) Development of parent-young interaction in asynchronously hatched broods of altricial birds. *Z Tierpsychol* 56:255–272
- Braun BM, Hunt GL Jr (1983) Brood reduction in black-legged Kittiwakes. *Auk* 100:469–476
- Bunnell FF, Dunbar D, Koza L, Ryder G (1981) Effects of disturbance on the productivity of White Pelicans in British Columbia – observations and models. *Colonial Waterbirds* 4:2–11
- Burger J (1974) Breeding adaptations of Franklin's gull (*Larus pipixcan*) to marsh habitat. *Anim Behav* 22:521–567
- Cooper J (1980) Fatal sibling aggression in pelicans: a review. *Ostrich* 51:183–186
- Din NA, Eltringham SK (1974) Breeding of the pink-backed pelican *Pelecanus rufescens* in Rwenzori National Park, Uganda. *Ibis* 116:477–493
- Dorward DF (1962) Comparative biology of the white booby and the brown booby *Sula* spp. at Ascension. *Ibis* 103:174–200
- Evans RM (1984) Some causal and functional correlates of creching in young white pelicans. *Can J Zool* 62:814–819
- Evans RM, Cash KJ Early spring flights of American white pelicans: timing and functional role in attracting migrants to a breeding site. *Condor* (in press)
- Hahn DC (1981) Asynchronous hatching in the laughin gull: cutting losses and reducing rivalry. *Anim Behav* 29:421–427
- Hamilton WD (1964) The genetical evolution of social behavior I. *J Theor Biol* 7:1–16
- Howe HF (1976) Egg size, hatching asynchrony, sex and brood reduction in the common grackle. *Ecology* 57:1195–1207
- Howe HF (1978) Initial investment, clutch size and brood reduction in the common grackle (*Quiscalus quiscula* L.) *Ecology* 59:1109–1122
- Johnson RF, Sloan NF (1978) White pelican production and survival of young at Chase Lake National Wildlife Refuge, North Dakota. *Wilson Bull* 90:348–352
- Knopf FL (1976) Spatial and temporal aspects of colonial nesting of the white pelican, *Pelecanus erythrorhynchos*. PhD Thesis Utah State University Logan Utah, pp 76
- Knopf FL (1979) Spatial and temporal aspects of colonial nesting of white pelicans. *Condor* 81:353–363
- Lack D (1947) The significance of clutch size. *Ibis* 89:302–352
- Lack D (1954) The natural regulation of animal numbers. Methuen, London
- Lack D (1968) Ecological adaptations for breeding in birds. Methuen, London
- McCrimmon DA Jr (1980) The effects of timing of breeding, dispersion of nests and habitat selection on nesting success of colonial waterbirds. *Trans Linn Soc NY* 9:87–102
- Meyburg BU (1974) Sibling aggression and mortality among nestling eagles. *Ibis* 116:224–228
- Mock DW (1984) Infanticide, siblicide and avian nestling mortality. In: Hausfater G, Hrdy SB, Vogel C, Dickeman M (eds) Proc Int Symp on Infanticide in Animals and Man. Special volumes of Ethology and Sociobiology
- Nisbet ICT (1975) Selective effects of predation in a tern colony. *Condor* 77:221–226
- Nisbet ICT, Cohen ME (1975) Asynchronous hatching in common and roseate terns *Sterna hirundo* and *S. dougallii*. *Ibis* 117:374–379
- Nuechterlein GL (1980) Courtship behaviour of the western grebe. PhD thesis University of Minnesota
- O'Connor RJ (1978) Brood reduction in birds: selection for fratricide, infanticide and suicide? *Anim Behav* 26:79–96

- O'Malley JBE, Evans RM (1980) Variations in measurements among white pelican eggs and their use as a hatch date predictor. *Can J Zool* 58:603–608
- Parsons J (1975) Asynchronous hatching and chick mortality in the herring gull (*Larus argentatus*). *Ibis* 117:517–520
- Schaller GB (1964) Breeding behavior of White Pelican at Yellowstone Lake, Wyoming. *Condor* 66:3–23
- Shugart GW, Fitch MA, Shugart VM (1981) Minimizing investigator disturbance in observational studies of colonial birds: access to blinds through tunnels. *Wilson Bull* 93:565–569
- Sloan NF (1982) Status of breeding colonies of White Pelicans through 1979. *Am Birds* 36:250–254
- Trivers RL (1974) Parent-offspring conflict. *Am Zool* 14:249–264
- Vestjens WJM (1977) Breeding behaviour and ecology of the Australian pelican, *Pelecanus conspicillatus*, in New South Wales. *Aust Wildl Res* 4:37–58