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

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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 that 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 nesting 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-