

BROOD REDUCTION AND AGGRESSIVE BEGGING BEHAVIOURS IN YOUNG
AMERICAN WHITE PELICANS

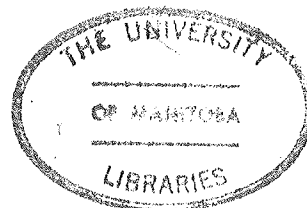
by

Kevin J. Cash

A thesis
presented to the University of Manitoba
in partial fulfillment of the
requirements for the degree of
Master of Science
in
Department of Zoology

Winnipeg, Manitoba

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ABSTRACT

Brood reduction and aggressive begging behaviours in young American white pelicans (Pelecanus erythrorhynchos) were studied in colonies at East Shoal Lake, Manitoba, during the summers of 1982 and 1983. Observations were conducted from a blind adjacent to the colony.

A hatching asynchrony of 2.5 days in 2-egg clutches resulted in a size gradient between chicks which facilitated sibling harassment and lack of feeds delivered to the subordinate chick.

A maximum of one young survived per nest. In marked broods, the second-hatched chick survived in 20% of successful nests. Manipulated clutch sizes revealed that the presence of a second chick contributed significantly to the reproductive success of the parents.

Results support the hypothesis that the second egg "insures" against early loss of the first egg or chick. Evidence was also found to suggest that the parent, by creating an asynchrony in hatch, by nonintervention in sibling aggression, and by feeding only the dominant chick, maximizes its chances of rearing the most viable young.

Aggressive behaviours occurring in association with feeding developed in chicks approximately three weeks of age. These behaviours involved aggression directed toward self (Convulsion) or conspecific young (Aggression).

Frequency of behaviours prior to feeding depended upon the duration of the begging bout. Behaviours given after the feed were not related to the duration of the feed but were dependent on the amount fed (as measured by throat distension).

A model is proposed to explain aggressive behaviours as manifestations of parent-offspring conflict over the initiation or continuance of feeding. The close association of these behaviours with both feeding and low-intensity begging suggests that they function primarily as begging displays or, for aggression, to drive other young away from the parent food source. Alternative functions of Convulsion and Aggression are not supported by data collected in this study.

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GENERAL INTRODUCTION

The general biology, breeding chronology, courtship behaviours and flocking of the American white pelican (Pelecanus erythrorhynchos) have been well documented (Behle 1958; Schaller 1964; Knopf 1976, 1979; O'Malley and Evans 1982a,b). Aspects of creching and thermoregulation in the young have been examined (Evans 1984a,b) but the details of most other chick behaviours and development have received little attention. This study examined the development of young white pelicans and their interactions with siblings, adults and conspecific chicks.

Although white pelicans typically lay two eggs, more than one young per nest is rarely reared each year (Johnson and Sloan 1978; Sloan 1982). Sibling aggression leading to the death of one chick has been suggested as the proximate cause of brood reduction in this and other pelican species (Schaller 1964; Cooper 1980) but the ultimate cause has not been determined. The "insurance-egg" hypothesis (Dorward 1962) provides a possible ultimate cause of brood reduction in the white pelican, but this hypothesis has yet to be studied in detail in any species (Mock 1984). The first objective of this study was to examine in detail the chronology and proximate causes of brood reduction in the white pel-

ican and to test, through manipulation, the insurance-egg hypothesis in this species.

White pelican chicks are brooded continuously for about the first three weeks of their lives. At that time parents begin to leave the colony, returning once a day to feed their own young (Schaller, 1964). At this time the chicks move out of the nests and gradually form large aggregations termed creches or pods (reviewed in Evans, 1984a). Behaviours termed Convulsion and Aggression (Burke and Brown, 1970), develop concurrently with creche formation. Both are observed in association with feeding and involve aggression directed toward conspecifics or self. The second objective of this study was to determine the occurrence, context and functional significance of Convulsion and Aggression observed during the creche period. For this thesis the sections on brood reduction and on Aggression and Convulsion are treated separately.

PART I. BROOD REDUCTION AND THE INSURANCE-EGG
HYPOTHESIS IN THE AMERICAN WHITE PELICAN

INTRODUCTION

The major hypothesis concerning the adaptive significance of brood reduction in birds, originally proposed by Lack (1947, 1954, 1968), suggested that females of many species produce clutches, and subsequently broods, of greater size than typical food conditions allow them to rear to fledging. Lack assumed that after hatching, brood size is adjusted to meet prevailing food conditions. Thus in years of high food availability the entire brood can be raised, but in years of average or lower food availability brood size is reduced and a smaller, but relatively fitter brood fledges. Lack further proposed that brood reduction is facilitated by the creation of different-sized nestlings with different competitive abilities. These differences are produced through asynchronous hatching, differing sibling hatch weights, or a combination of the two. Variations of this type generate a competitive or size hierarchy which, in times of food shortage allow for a quick and efficient elimination of smaller (typically younger) brood members at a minimum cost to parents and surviving siblings.

Many studies on 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. Due to its inability to compete successfully or defend itself the last-hatched sibling typically 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 or last laid egg is laid 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, but 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.

The cost to the parent adopting the insurance-egg strategy is presumably low since the energetic cost of producing

an "extra" egg is offset by the increase in net production of young (Kepler 1969). The cost to the surviving sibling is also low since, by the mechanisms discussed above a competitive hierarchy is established allowing for an early and efficient elimination of the younger chick should the older young survive. Implicit to any argument proposing an insurance-egg as the sole or primary pressure leading to the evolution of a larger clutch is the assumption that the probability of rearing the entire brood to fledging is very low. Such being the case, costs (in terms of the inclusive fitness of surviving young and parents) associated with the death of one chick would be minimal (O'Connor 1978).

Lack's original "food-related" hypothesis of brood reduction and the insurance-egg hypothesis are in no way mutually exclusive and in some species may act in concert in the evolution of clutch size (Nisbet 1975; Nisbet and Cohen 1975). Unfortunately the effects of each selective force are difficult to isolate when the two operate at the same time. While the former hypothesis has been extensively studied (see above), the latter has yet to be examined in detail (Mock 1984). The purpose of this study, therefore was to examine the insurance-egg hypothesis in white pelicans.

Sibling harassment leading to the death of one chick has been documented in several species of African eagles (Meyburg 1974, 1978; Brown et al., 1977; Gargett 1977, 1978, 1982), the south polar skua Catharacta maccormicki (Young

1963; Spellerberg 1971; Procter 1975), two species of booby (Dorward 1962; Nelson 1967; Kepler 1969) and in most species of pelicans (reviewed in Cooper 1980).

Species for which the insurance-egg has been invoked as the sole or primary explanation of clutch size generally have several characteristics in common: (1) most are relatively large, (2) their nestling periods are long, (3) their typical clutch, and initial brood size is two, (4) both chicks rarely fledge and (5) sibling harassment leads to the early death of one chick from starvation, injury or exposure.

The white pelican would appear to be an ideal species in which to examine the insurance-egg hypothesis. 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). In many colonies average productivity of less than one chick per brood has been recorded (Sloan 1982). Furthermore, sibling harassment leading to the death (by starvation or exposure) of one chick (siblicide) would seem to be the mechanism by which the brood is reduced (Schaller 1964; Knopf 1979).

To test the insurance-egg hypothesis in white pelicans I documented (1) the behaviour of chicks and adults associated with brood reduction, including the timing of siblicide rel-

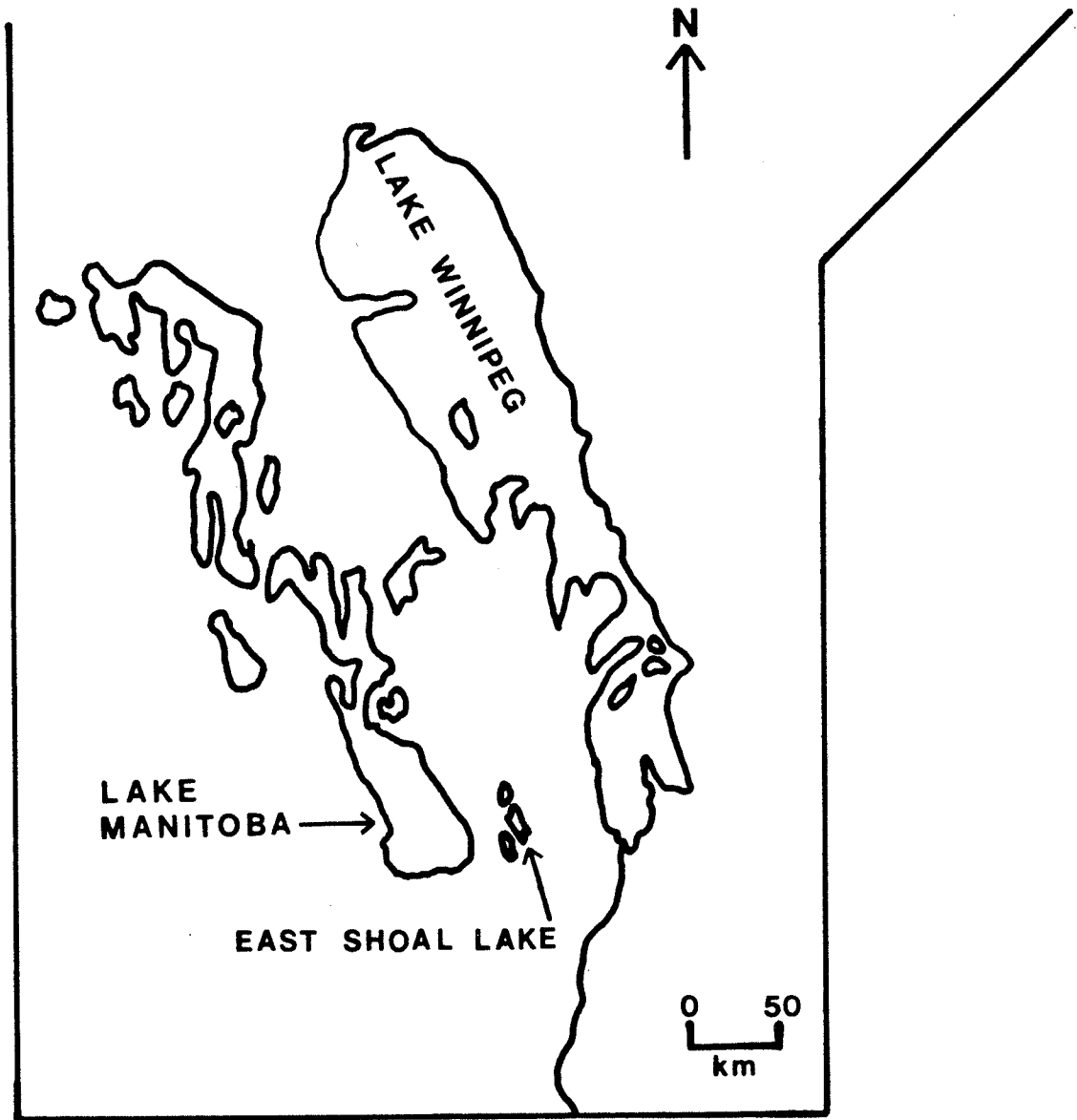
ative to the hatch of the second chick and the nature and context of sibling harassment, (2) the frequency of second chick survival and death of the older chick, (3) I also manipulated nest contents to produce clutches and broods of 1, 2 and 3 offspring to test the effect, if any, of the supposed insurance-egg on the hatching success and productivity of white pelicans.

STUDY AREA AND COLONY

The present study was carried out on white pelicans breeding on an island colony in East Shoal Lake, Manitoba in the summers of 1982, and 1983. East Shoal Lake ($50^{\circ} 22'N$, $97^{\circ} 36'W$) is a shallow body of water, approximately 6 km long and 3 km wide, which lies on a north-south orientation between Lakes Manitoba and Winnipeg (Fig. 1). Connected to North and West Shoal Lakes until late in the nineteenth century, East Shoal Lake is now separated from them by a series of low ridges (Taverner 1919). Having no definite inlet or outlet the lake's water levels fluctuate widely according to annual variations in precipitation and runoff (Taverner 1919; Evans 1972). Consequently, colony size is also subject to fluctuation as changing water levels influence the number and size of suitable nesting islands (Evans 1972).

Though the existence of the East Shoal Lake pelican colony was noted as early as 1878 (see Taverner 1919) it was not until 1962 when Hosford (1965) estimated a breeding population of 300 pairs that the colony was reliably censused.

Fig. 1. Map of southern Manitoba showing the location of East Shoal Lake



since then the population has grown steadily and consisted of 1237 pairs in 1983.

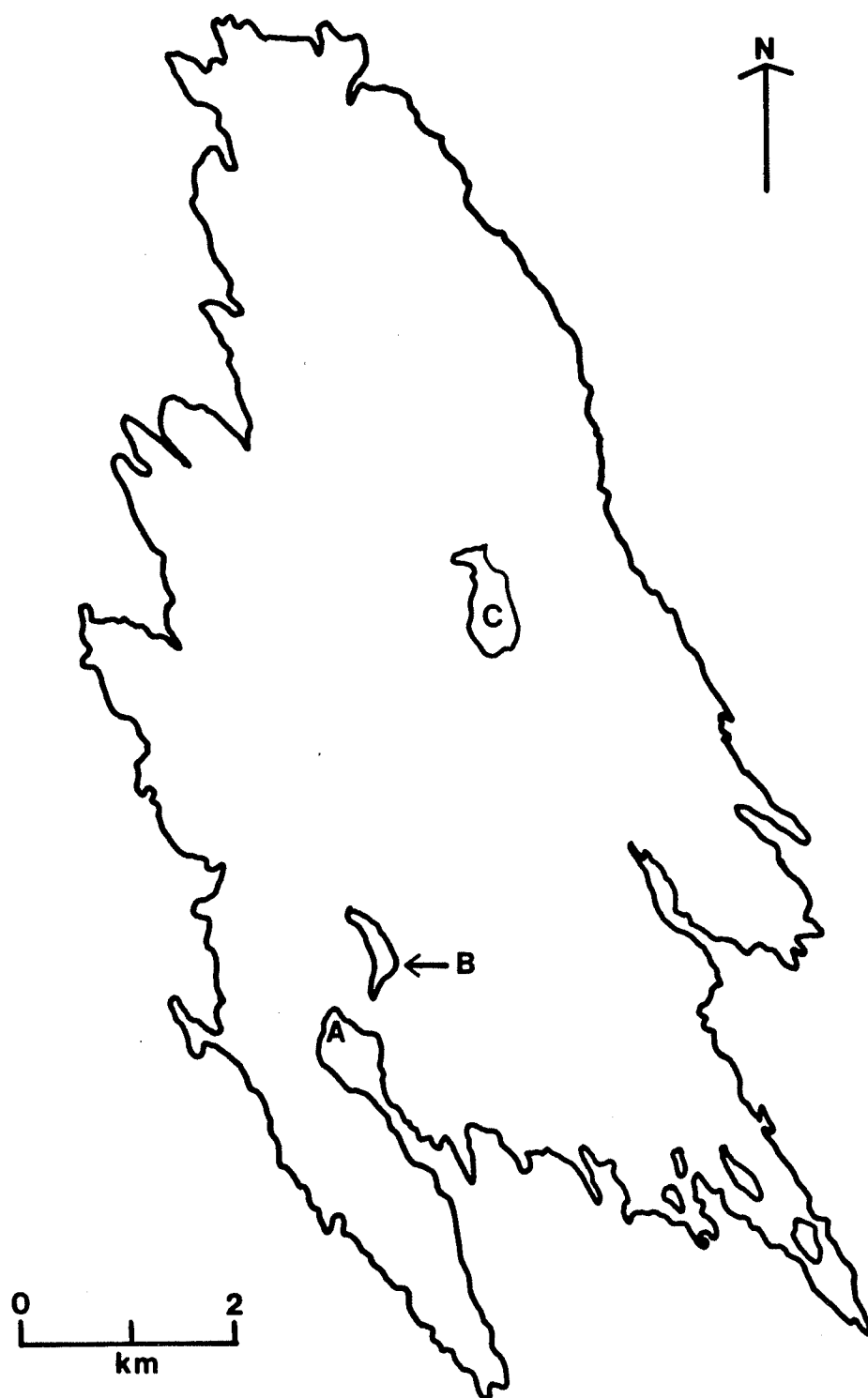
In 1982 pelicans nested in three locations on East Shoal Lake. A colony of 256 nests, situated at the tip of a narrow peninsula jutting out from the southern shore of the lake (A in Fig. 2), was used for my study in 1982. Two colonies, on islands (B and C, Fig. 2), were first occupied in 1982 and contained 577 and 623, nests respectively.

The abandonment of colony A and an increase in available nesting sites on the islands correlated with lower water levels in 1983. Colonies B and C contained 655 and 582 nests respectively. All 1983 data were collected from colony B.

Islands B and C are narrow gravel bars and though their sizes fluctuate greatly with changing water levels they are seldom more than 2 m above water level. Phragmites australis and Carex spp. were the predominant plants on both of the islands. Colony A also contained these species plus Hordeum jubatum, Rumex spp. and other grasses (O'Malley 1980).

In both years pelicans were observed at the colony site by the third week of April, at least 10 days before the lake was ice free. Pelicans arrived at the colony on or about the day the species was first seen in the Province each year. Egg laying commences four to five days after arrival at the colony, and is followed by 31 to 32 days of incubation (Knopf 1976, 1979).

Fig. 2. Map of East Shoal Lake showing breeding colonies (A, B and C)



Each colony was comprised of from 1-11 highly synchronous subcolonies. Nests within subcolonies were separated by a distance approximately twice the adult bill length. Groups of nests separated by a distance more than twice the mean internest distance within subcolonies were designated as separate subcolonies (after O'Malley and Evans 1980).

MATERIALS AND METHODS

During the early part of each breeding season the colony was observed from a distance of approximately 2 km to determine the onset of breeding for each year. About six days prior to the expected hatch date a blind was erected at the edge of the colony, at least 5 m from the nearest nest. Erection of the blind at this time enabled me to choose the most appropriate observation position and at the same time minimize the probability of nest desertion due to my presence.

In 1982 the blind was located on the border of colony A and was accessed through a 40 m, above ground, plastic tunnel (Shugart et al. 1981). In 1983 the blind and a shorter tunnel system (8 m) was erected on the southern tip of colony B. Access to the tunnel was by use of a floating "muskrat lodge" blind (Nuechterlein 1980). These systems allowed me to enter the blind without being seen by the pelicans.

Behavioural Observations

Observations of nests began 2-3 days prior to hatch initiation and continued daily until creches formed when the young were about 20 days old. In 1982, 114 h of observations were made from 1 to 22 June while in 1983, 98.5 h of observations were made from 1 to 24 June. The focal-point (Altmann 1974) method of data collection was used, each observation nest ($n=37$ in 1982, 35 in 1983) being watched for 15-min periods. Observations were made with the unaided eye, 7 x 35 binoculars, or a 10-x spotting scope. The duration of aggressive encounters (see below) were timed to the nearest second with a stopwatch.

Data collected for each nest were: (1) the time between hatching of the first and second chicks, to identify and quantify hatching asynchrony, (2) feeding frequency, (3) when visible, prey size, as estimated from adult bill length, (4) recipient of feed (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.

Hatching date of each egg, and timing of brood reduction and creche formation were obtained for 13 nests in 1982,

32 in 1983. In all analyses for which no significant difference occurred between years, the data have been lumped.

Brood Reduction and Survival of Marked Broods

In 1983, two subcolonies approximately 50 m from the observation nests were selected for marking and experimental manipulation. Experimental broods were always approached from a direction opposite that of the observation nests. At no time during the censuses could the birds on the observation nests see me.

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 had 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 allow me to associate them with individual nests.

Egg and Brood Success at Manipulated Nests

On 19 May, approximately 13 days before hatching began I manipulated 60, 2-egg clutches to produce 20 matched triads of nests, each triad containing clutches 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 to suggest a significant difference in viability between first and second laid eggs (O'Malley and Evans 1980), I did not distinguish between them. Because subcolonies of pelicans are highly synchronized (Knopf 1979) I assumed that the egg added to nests to produce 3-egg clutches, did not differ markedly in its laying date.

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. To allow me to examine survival after hatching in broods of 1, 2 and 3 chicks, 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) indicate that white pelicans rarely raise more than one young to the creche stage. For purposes of analyses 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.

RESULTS

Behavioural Observations

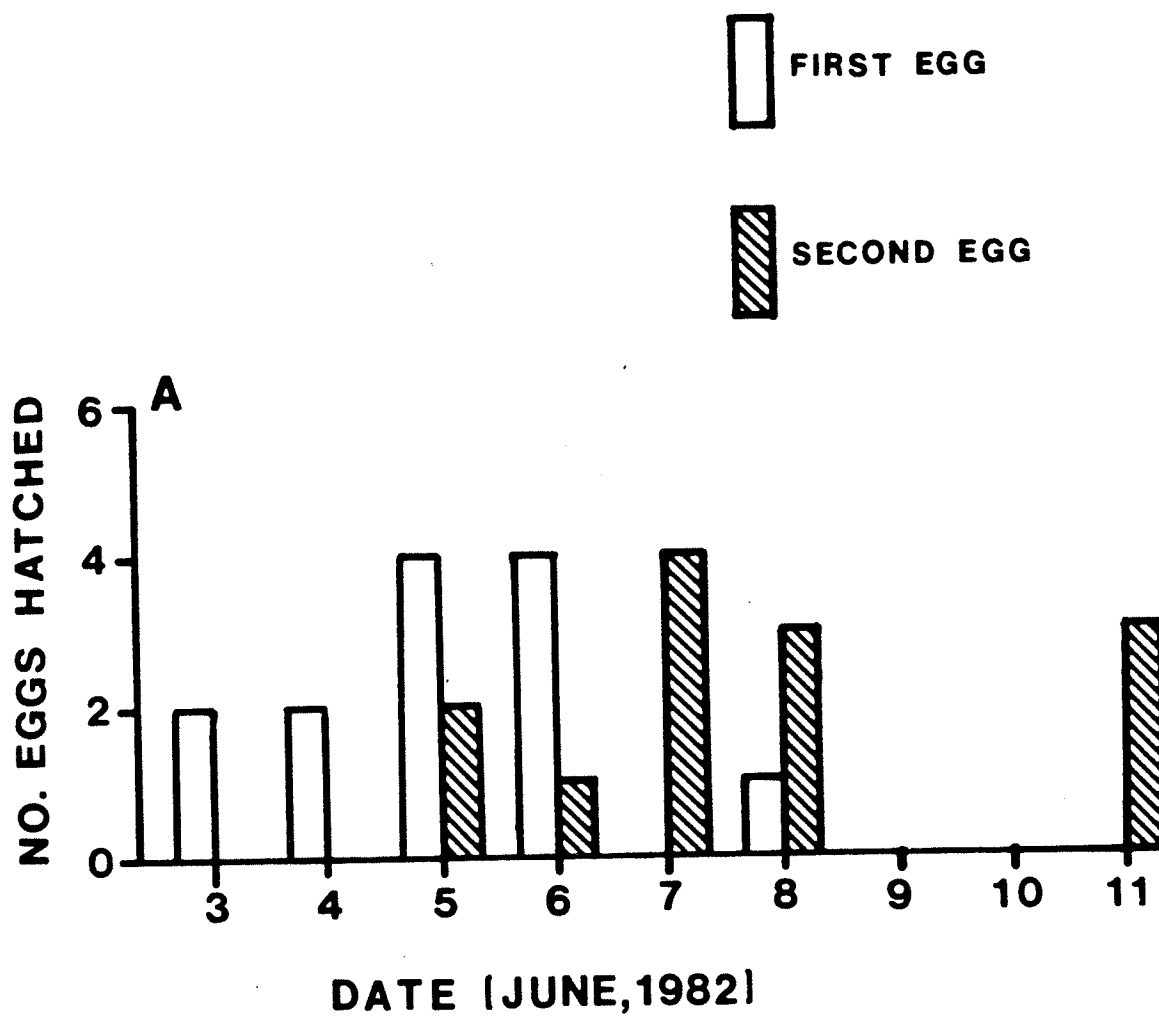
Of the 37 nests observed in 1982, 24 (64.9%) were deserted. All of these clutches involved apparently infertile eggs which were incubated up to 17 days after the expected date of hatch. The timing and spatial pattern of nest abandonment was apparently random. The fact that this was the last colony formed in 1982 may indicate the presence of inexperienced or inefficient breeders. In 1983, of 35 nests observed, only three (8.6%) were deserted, although the pattern was similar to that observed in 1982.

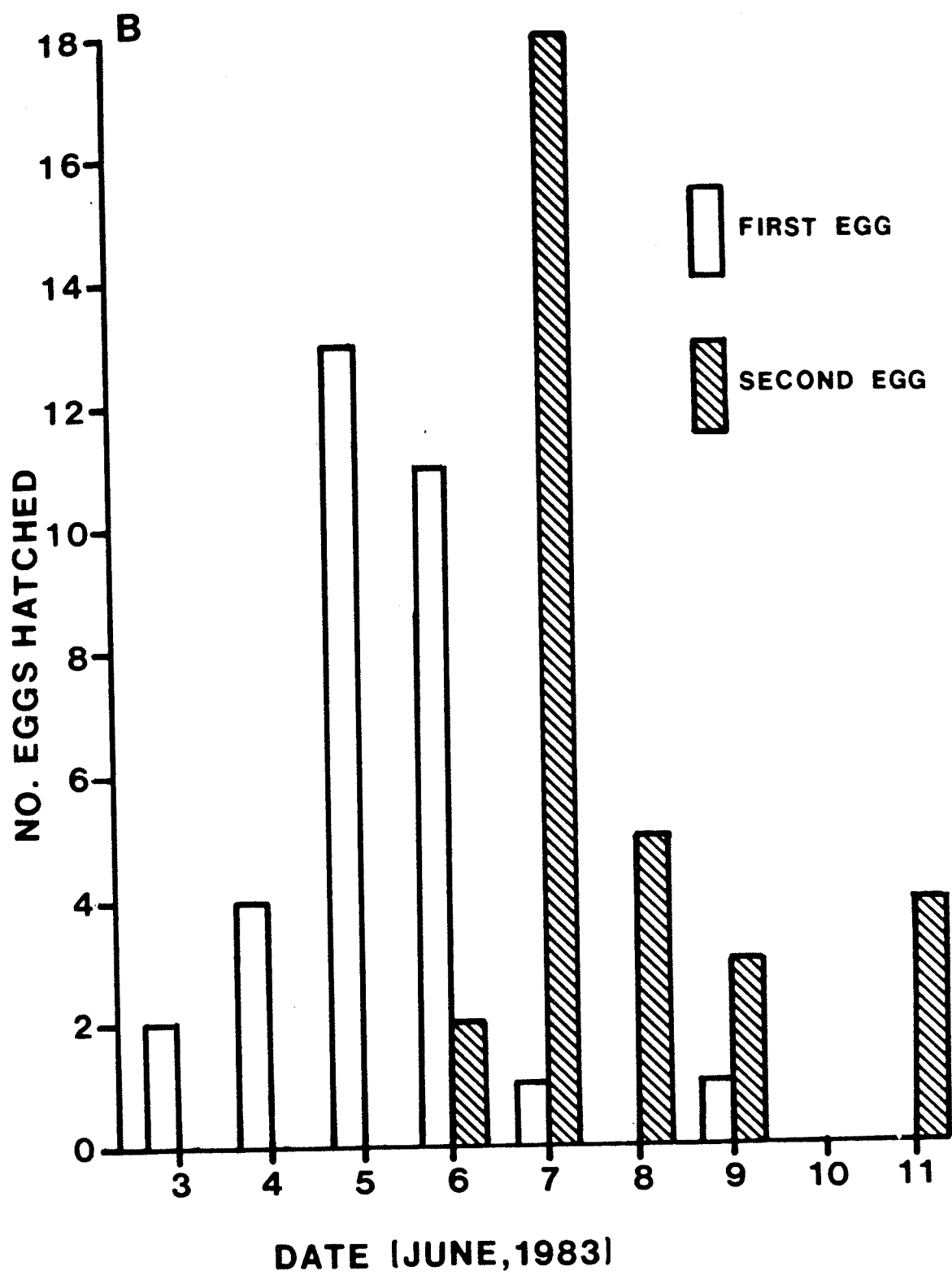
Hatching at observation nests began in both years on 3 June and was completed by 11 June (Fig. 3). The degree of hatching asynchrony within nests did not differ significantly between years ($t=0.27$, $p>.05$) and averaged 2.5 ± 1.1 (SD) days ($n=45$).

Feeding in relation to position of chick in nest

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 sibling remained toward the rear of the brooding parent. The larger young often was observed

Fig. 3. Hatch dates of first and second eggs in 1982 (A) and 1983 (B).





to prevent the smaller chick from moving forward (aggression described in detail below).

At this stage, adults fed the young by regurgitating small pieces of food into the pouch. The young then fed from the tip of the parent's lower mandible. From its more anterior position, the larger young had better access to these feedings. 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 lack of feedings directed toward the smaller sibling was also evident in its lack of growth as estimated by eye in most of the nests. Little growth was also characteristic of the smaller young in most other nonobservational nests checked during this period.

Adults normally made no obvious attempts to feed the most posteriorly positioned chick. On several occasions they ignored intense begging from the posterior most chick. 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 I saw the smaller chick fed exclusively.

Context and description of harassment of siblings

Sibling harassment was infrequent except when the brooding parent rose to stretch or preen. Of 18 such occasions, harassment of one chick by its sibling was noted in 17 (94.4%). If aggression occurred while the young were being brooded I was unable to detect it.

When an adult stood up, both young were typically in the forward half of the nest. The larger chick then pecked its sibling about the head, particularly the eyes, and 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 other, nonobservational nests were examined in other parts of the colony. The duration of aggressive bouts between siblings ranged from 34-300s ($\bar{x}=126.9$, $n=17$). Aggression typically terminated when the smaller chick retreated toward the rear of the nest or the adult resettled on the chicks. Only twice did adults intervene to prevent sibling aggression, on both occasions the adults in question were attempting to resume brooding.

Continued harassment and 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 in other parts of the colony indicates that death by exposure may occur.

Thus, broods were reduced in nests under observation because the second, smaller chicks starved or sometimes died of exposure but not because of injuries caused directly by sibling harassment.

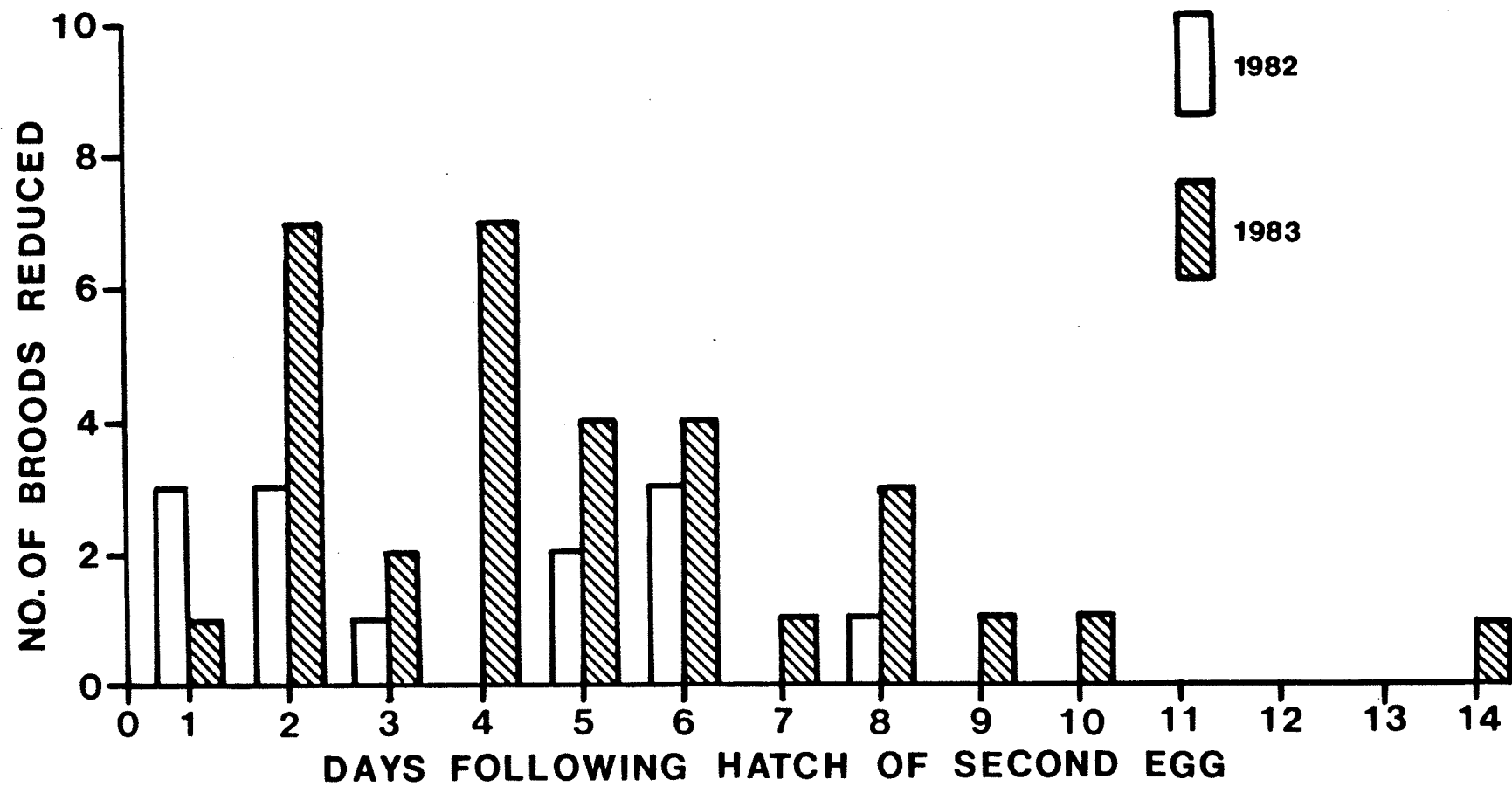
Timing of brood reduction

In 1982 the mean period between hatch of the second young and the occurrence of brood reduction was 3.7 ± 2.39 days ($n=13$ nests). The time until chick death in 1983 was 4.9 ± 2.84 days ($n=32$ nests), slightly but significantly longer than in 1982 ($t=1.793$, $p<.05$, Fig. 4).

Predation

Herring gulls (Larus argentatus), ring-billed gulls (L. delawarensis) and striped skunks (Mephitis mephitis) scavenged for dead chicks and deserted eggs, but no evidence for predation on live chicks was obtained in either year.

Fig. 4. Time between hatch of the second egg and brood reduction in 1982 and 1983.



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. None contained more than one chick. The average time period between hatch of the second chick and reduction in brood size by one was 6.5 ± 2.38 days (Fig. 5). Since broods were checked once every two days, this figure could be biased upward by as much as two days.

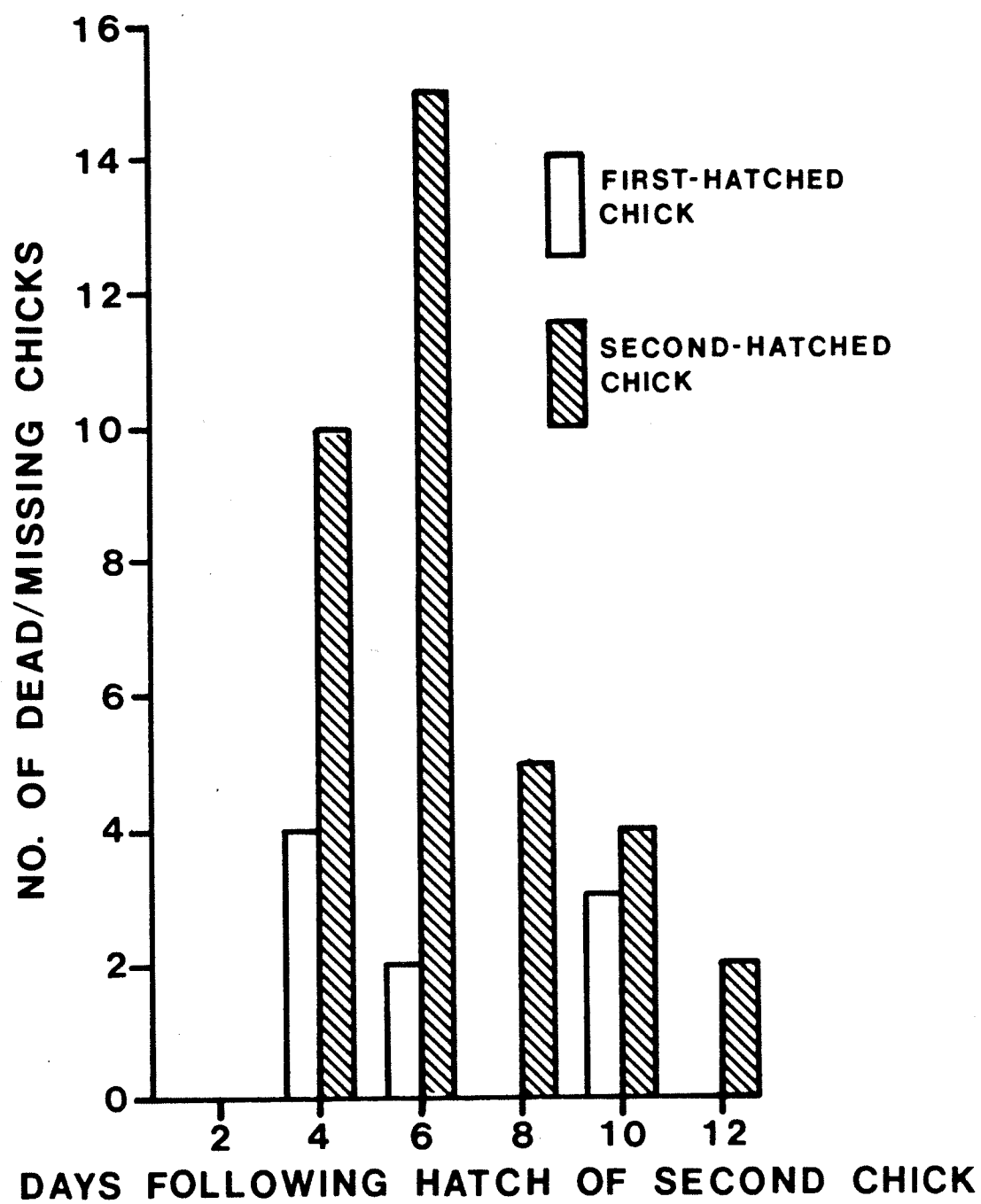
In four of the five nests that failed, both chicks disappeared over the same census period, which may indicate desertion by the adults. The possibility of chick loss to gulls following the census but prior to the return of adult pelicans to the nest cannot be totally ruled out. My observations of both pelicans and gulls as I left the area suggested however, that the brooding adults normally 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. These chicks survived advantages in size (estimated to be as much as 60%) and mobility possessed by the older chick at the time the younger

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

Brood status	n	%
Younger chick missing or dead	36	72
Older chick missing or dead	9	18
Both chicks missing or dead	5	10
Both chicks present	0	0
TOTAL	50	100

Fig. 5. Timing and victim of brood reduction in marked broods.



bird hatched. I found 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, $p > .05$).

Egg and Brood Success at Manipulated Nests

The proportion of eggs which hatched successfully in each nest did not vary significantly with clutch size ($\chi^2 = 0.151$, $p > .05$ Table 2). For 2-egg clutches, 16 (80.0%) hatched both eggs while one nest (5.0%) hatched only one egg. In 3-egg clutches, 15 (75.0%) hatched all three eggs while 2 (10.0%) hatched two eggs. At least one egg hatched in 17 (85.0%) of the nests of each clutch size (Table 2).

Nine nests (15.0%) failed (3 of each clutch size) because the adults deserted them between the time of clutch manipulation and the first census 13 days later. The influence, if any, of clutch manipulations on nest desertion is not known, but should have been the same for 1, 2 and 3-egg clutches.

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 unlikely that

Table 2. Hatching success of manipulated clutches

Situation	clutch size		
	1(20) ¹	2(20) ¹	3(20) ¹
No. of clutches that hatched			
1 egg	17	1	0
2 eggs	1	16	2
3 eggs	0	4	15
No. of eggs hatched (%)	17(85.0)	33(82.5)	49(81.7)
No. of successful ² nests (%)	17(85.0)	17(85.0)	17(85.0)

¹Sample size²Success in the hatching of at least one egg per nest

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 (Table 3) revealed that the number of successful broods differed significantly with brood size ($\chi^2=6.74$, $p<.02$, for all broods combined). Success of broods which originally containing one vs. two chicks (47.1% vs. 88.2%) differed significantly ($\chi^2=6.58$, $p<.02$). Broods of three, with a success rate of 70.6% were intermediate and did not differ significantly from broods of one ($\chi^2=1.94$, $p>.05$) or two ($\chi^2=1.62$, $p>.05$).

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 ($\chi^2=4.48$, $p<.05$).

Table 3. Survival of chicks (18 ± 3 days old) in manipulated broods

	Brood size		
	1	2	3
No. of broods	17	17	17
No. of successful ¹ broods (%)	8(47.1)	15(88.2)	12(70.6)

¹Success 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).

DISCUSSION

To my knowledge this study constitutes the first direct test of the insurance-egg hypothesis, as well as the first detailed examination of sibling aggression and brood reduction in any species of pelican. 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 3) 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 proportion of eggs in 3-egg clutches which hatched successfully (81.7%) was unexpectedly high. White pelicans incubate with their feet (Schaller 1964; pers. ob.) and

were not expected to incubate 3-egg clutches successfully. However, the fact that broods of two were marginally more successful than broods of three (88.2% vs 70.6%) may indicate that clutches of two are optimal.

The mortality rate of first-hatched chicks in unmanipulated broods of two (28.0%, Table 1) was appreciably lower than for young in broods of one in the manipulation experiment (52.9%, Table 3). The trend, though not significant ($\chi^2=3.5$, $p>.05$), suggests that a second chick may indirectly enhance the survival of its sibling. This would occur if, for example, parental behaviour toward the brood is influenced by the presence of the second young. Since the blind was intentionally located well away from the manipulated nests I was unable to test this. An alternate possibility, that first and second eggs or chicks differed in viability, is not supported by evidence from the laboratory (O'Malley and Evans 1980).

The young were still relatively small when brood reduction occurred, as were food demands placed on parents. Dominant chicks were never observed to beg without gaining access to the parents' pouch and parents appeared capable of delivering sufficient amounts of appropriately sized food to the chicks.

Delivered food most often consisted of small chunks (<10 cm long) of partially digested fish. Only twice (3.64% 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. 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 a 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. Proof of food limitations in pelicans at any stage is lacking.

As mentioned earlier the insurance-egg and food-related hypotheses of brood reduction are not mutually exclusive and may act together in the evolution of larger clutch size. 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 white pelican chicks survive in up to 10% of the nests is consistent with this interpretation. The large number of 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 concerning the thresholds at which fratricide (siblicide), infanticide and suicide are favoured for different brood sizes. The model allows O'Connor to make several predictions. One of these predictions is: "Sibling rivalry and aggression should be most apparent in small broods." He also predicted that conflict between the adult and potential survivor would be most intense in small broods. Finally, O'Connor also noted that such conflict would manifest itself most readily in parental intervention to prevent sibling aggression.

O'Connor's prediction seems consistent with kin-selection and parent-offspring conflict theories, yet I found the parents I observed did not intervene to prevent sibling aggression. Nor has such intervention been noted in pink-backed (Pelecanus rufescens) (Din and Eltringham, 1974) or Australian (P. conspicillatus) (Vestjens 1977) pelicans or in several species of African eagles (Meyburg 1974).

I believe 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, arises 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, because it is more related to itself than to its sibling or parent, 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 the potential survivor ends. My results suggest that this point of non-conflict between parent and potential survivor was the norm in the colony I studied.

In those species in which the "extra" egg serves primarily or exclusively as insurance against early loss of the first chick, the probability of rearing both young is low or negligible and the parent would never be selected to invest equally in both chicks. Thus, although conflict might arise as to which chick is to survive, there would be no conflict over how many chicks would survive.

Given that the parent can rear only one chick it should benefit most by rearing the more viable young. Nonintervention in sibling aggression leading to the death of the weaker chick would thus appear to be an adaptive parental strategy in white pelicans. By establishing dominance quickly, the survivor also benefits, presumably by reducing its chances of becoming the victim or being weakened as a result of a drawn-out contest.

Asynchronous hatching and the resulting size differential may provide a mechanism by which the adult is ensured of a viable survivor. Under the proper degree of asynchrony, a typical or adequately viable first chick could quickly dispatch the younger bird, at a minimum cost both to itself and the parent. The slight but significantly larger size of first-hatched eggs in this species (O'Malley and Evans 1980) would be expected to facilitate the competitive advantage of the older young. Should the first chick be less than adequately viable, however, the second young would be more likely to overcome its size disadvantage and kill its sibling. The adult, by not interfering in aggression and by feeding only that chick in the dominant position, contributes to the increasing disparity between chicks and thus shortens the period between hatch and brood reduction.

SUMMARY

Mortality rates of 28.0% among first-hatched chicks in broods of two and of 52.9% in broods of one chick, combined with a survival rate of 20% among second hatched chicks in broods of two provide evidence for the existence of an insurance-egg or chick in white pelicans. Manipulation experiments revealed that the presence of an insurance-chick made a significant contribution to the adult's reproductive success and constitute proof of the hypothesis.

Broods are reduced through sibling harassment which leads to the death of one chick by starvation or exposure within 4.5 days after the second young hatched. The parent, by not intervening to prevent sibling aggression and by feeding only the more anteriorly positioned young, a position defended by the dominant chick, ensures that the more viable young survives. Asynchrony in hatch averaging 2.5 days creates a competitive gradient among chicks such that a viable older chick can quickly eliminate its sibling while at the same time a younger chick could overcome its disadvantages in size and usurp its older sibling should the latter be less viable.

Finally the parent-offspring conflict predicted by O'Connor (1978) was not observed in this study. Nor is it predicted to occur in those species in which "insurance" is the sole or primary selective pressure favouring the evolution

of clutch size beyond the number which can be normally reared to fledging.

PART II THE OCCURRENCE, CONTEXT AND SIGNIFICANCE
OF CONVULSION AND AGGRESSION IN YOUNG AMERICAN
WHITE PELICANS

INTRODUCTION

Approximately three weeks after their young have hatched, adult pelicans begin to leave them unattended throughout much of the day. Simultaneously, the young begin to form into large "pods" (Schaller 1964) or creches (Evans 1984a).

Thereafter, young receive one feeding a day, each parent returning to the colony for less than 5 min every two days (Schaller 1964). When an adult lands in the colony it walks past or through the creche until approached by its begging chick. Feeding is usually initiated quickly, typically a few meters away from the creche (Schaller 1964; Evans 1984a). Parent-offspring recognition, though poorly understood appears to be mutual and well-developed by the creche stage (Schaller 1964). Concurrent with the formation of the creche, young white pelicans develop the so called "convulsion" display (Burke and Brown 1970). This behaviour is observed in association with feeding of the young by a parent, and involves aggression directed toward other chicks or toward self.

First noted in white pelicans by Finley (1907), who described the displaying chick as appearing "raving mad", convulsions have since been documented in the brown (P. occidentalis) (Chapman in Bent 1964), pink-backed (Burke and Brown 1970; Din and Eltringham 1974) and the Australian (Vestjens 1977) pelican. Though well documented and frequent in all these species, the context and functions of this behaviour have not yet been addressed.

The objective of this portion of my study, therefore, was to determine the occurrence, context and functional significance, if any, of convulsions in young white pelicans. To fulfill these objectives detailed observations on the frequency and timing of Convulsion and Aggression in relation to feeding of the young by a parent were made on both marked and unmarked birds.

For the purposes of this paper I will divide convulsions into two parts: Convulsion (apparent aggression directed toward self), and Aggression (directed at other young), and treat them separately as distinct behaviours.

The terms "Convulsion" and "Aggression" are used below in a purely descriptive sense. These terms have no implications with respect to the physiological state, motivation, or function of the behaviours.

MATERIALS AND METHODS

These studies were carried out on white pelicans breeding on East Shoal Lake, Manitoba in the summers of 1982 and 1983 (see Part I for description).

Behavioural Observations

Observations were begun at the time of creche initiation and continued until the young were about nine weeks old, approximately two to three weeks before they left their nesting island (Beaver and Lewin 1981). In 1982, 160.5h of observations were made between 23 June and 7 August while in 1983, 84.5h of observations were made from 25 June to 8 August. Though observations were taken during all daylight hours most were concentrated between 1000 and 1700h when most feedings take place (Evans 1984a). Observations were made with the unaided eye, 7 x 35 binoculars or a 10 x spotting scope. Durations (see below) were timed to the nearest second with a stopwatch.

As Convulsion and Aggression normally are associated with feeding of the young (Schaller 1964), I collected data by scanning the colony area for incoming adults. Each adult-young pair was then observed until the parent left the colony area. I recorded the following data for each feeding bout: (1) time of day, (2) duration of begging bout, i.e., the time between arrival of the adult on the colony and ini-

tiation of feeding (1983 only), (3) the occurrence and order of Convulsion and Aggression prior to feeding, (4) the duration of the feed, i.e., the period the chick's head spent in the parental throat, (5) the occurrence of a distended esophagus or throat in the chick following the feed, (6) the occurrence and order of Convulsion and Aggression following a feed, (7) the period the adult remained in the colony following a feed (1982 only), and (8) response of displaying chick upon departure of the adult (1982 only).

Multiple feedings of a single chick separated by less than 5 min were recorded as a single feeding bout. The sum duration of all component feeds was recorded. Only those displays preceding the first and following the final feeding were noted. Multiple feedings of a single chick separated by more than 5 min were recorded as separate feedings.

Complete records were obtained for 1143 feedings (600 in 1982, 543 in 1983). In all analyses for which no significant differences occurred between years the data were lumped.

Also, 45 feeds were filmed on Kodachrome 40 Super 8 film. These films were analysed later to obtain the duration of Convulsion and Aggression.

Marking of Adults

The frequency with which each parent returned to the colony to feed its young was determined by colour marking one member of each of eight breeding pairs. On 21 June, 1983, late in the nestling period, I approached, in a mobile blind, to within 2 m of brooding adults. Adults were then sprayed with a solution of Malachite Green and water ejected from a large syringe. Characteristic markings (e.g. scarred pouch, bare patch) possessed by one member of each of an additional five adult pairs allowed me to distinguish between the members of 13 pairs overall. All subsequent feeds delivered by marked adults were noted.

Sprayed adults lost their markings prior to creche formation. All observations were therefore made on characteristically marked adults.

Colour Marking of Young

Early in the creche period of each year (29 June 1982, 27 June 1983) young were herded into a corral made of 1 cm mesh fish seine and individually marked with small flags. Flags consisted of soft nylon-coated vinyl plastic strips ("Saflag", Safety Flag Co. of America), 9 cm by 3.5 cm, which bore individually identifiable letter-number combinations. A flag was affixed between the scapulae of 53 chicks in 1982 and 30 in 1983 using a surgical needle and nylon su-

ture thread to make a single stitch. Flags sloughed off from 3-40 days after marking. The identity of all marked chicks involved in observed feedings was noted.

RESULTS

Behavioural Observations

Convulsion and Aggression in creche-aged young occurred only in the presence of an adult and in association with a feeding. Most feedings took place near mid-day (Fig. 6) and about 90% of them were preceded or followed by Convulsion, Aggression, or both (Table 4).

Description of Convulsion

Convulsions were typically performed in front of the adult. Early in Convulsion the chick began to rock or shake its head through a wide arc while emitting begging calls. The chick then dropped down, crouching on its tarsi or laying on its side. Change in posture was followed by flapping of one or both wings either against the substrate or, if the bird was on its side, through a skyward directed arc. Head rocking and vocalizations were maintained through the entire Convulsion. The young commonly snapped its bill rapidly and in some instances grasped and "gnawed" its own wing.



Fig. 6. Timing of 1318 feeds during the creche period.

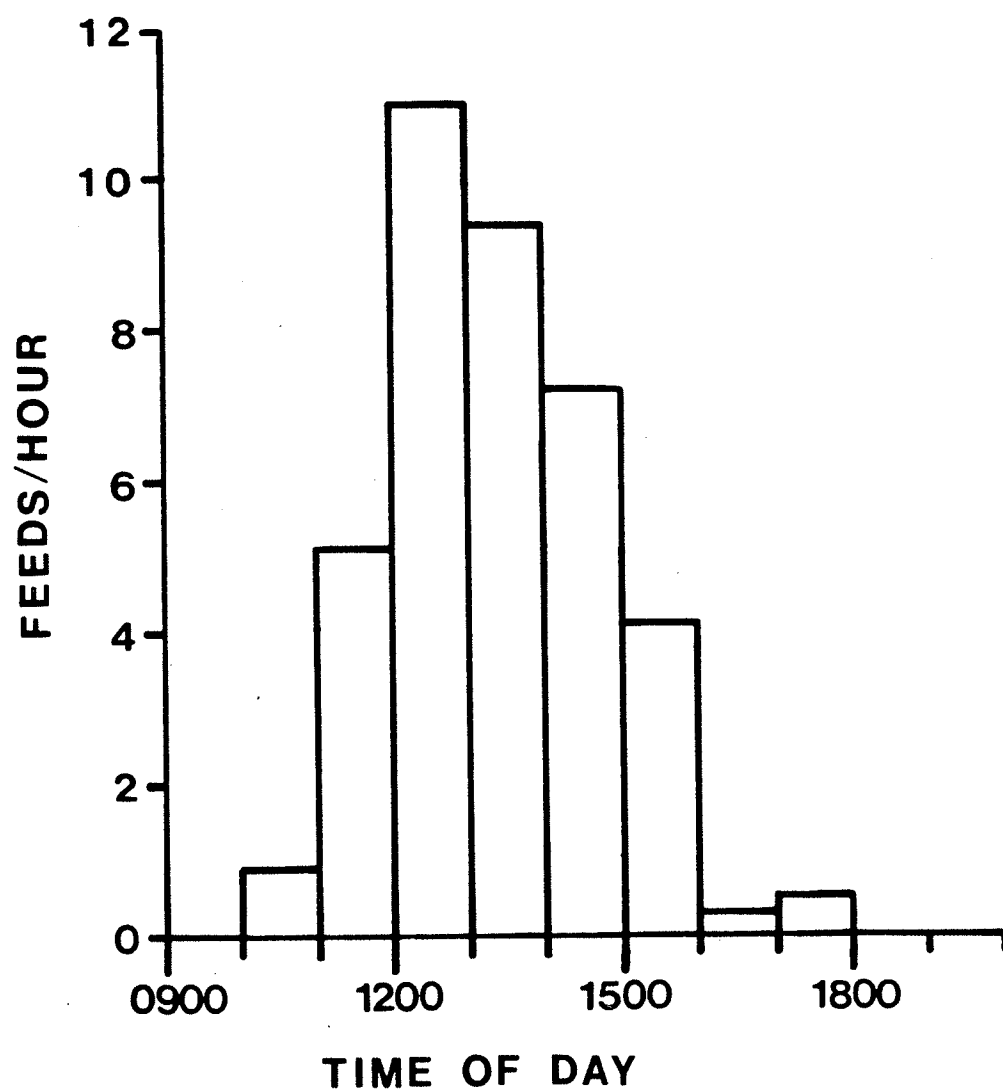


Table 4. Association between feedings and Convulsion or Aggression in 1982 and 1983

Behaviour	1982 n (%)	1983 n (%)
Feedings preceded and/or followed by both Convulsion and Aggression	238 (39.7)	247 (45.5)
Feedings preceded and/or followed by Aggression only	204 (34.0)	183 (33.7)
Feedings preceded and/or followed by Convulsion only	85 (14.2)	63 (11.6)
Feedings not preceded or followed by Convulsion or Aggression	73 (12.2)	50 (9.2)
TOTAL	600 (100.0)	543 (100.0)

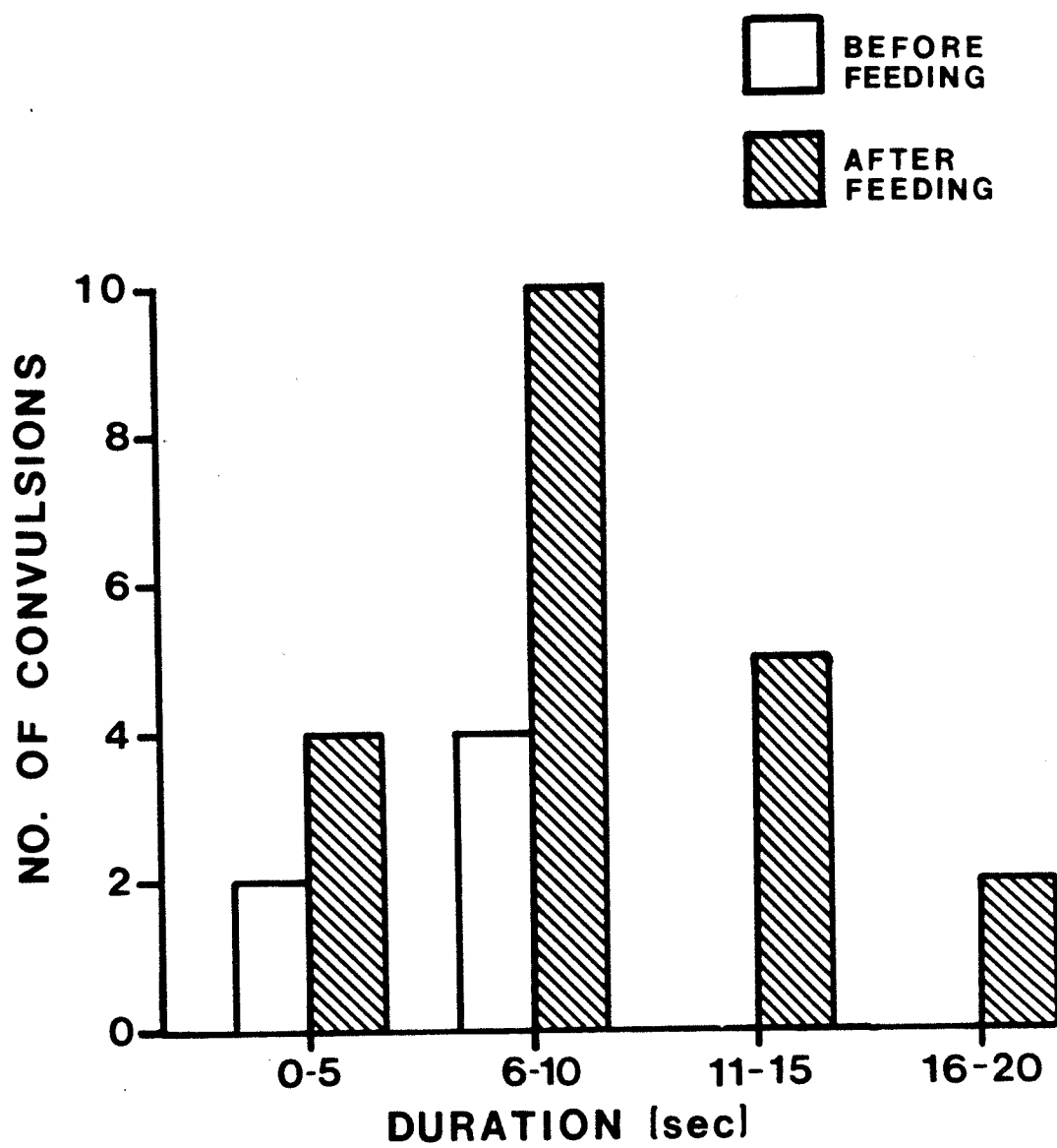
Certain chicks displayed Convulsion-like behaviours toward adults other than their own parents. These involved head-wagging, bill-snapping and vocalizations but at a much lower intensity than that seen in parent-directed Convulsion. Nor did birds giving these displays drop down to lay on their tarsi or side. Convulsion directed at non-parents was not common except in a few individuals (three to four chicks in each year), which directed the display toward almost all in-coming adults. Only those chicks which dropped down to lay on their side or tarsi are included in the analysis presented here.

The duration of Convulsion given before or following a feeding did not differ significantly ($t=0.98$, $p>.05$). It lasted from 3-17 s ($\bar{x}=8.7$, Fig 7.). When Convulsion was occurring at the time the adult left the colony the convulsion typically (96.8% of 185 observations) ended within 3 s.

Description of Aggression

Aggression involved running towards other chicks, but not adults. While running, the aggressive chick's bill was commonly snapped rapidly, the wings were extended and "lunges" were directed toward one or more other birds. Contact with other young was infrequent, being observed only when two simultaneously aggressive chicks met. Aggression apparently was directed toward any young which happened to be in a given area (usually those near the presumed parent) rather than

Fig. 7. Duration of Convulsion before and after feeding.



toward a particular individual. Lack of any specificity between participants was verified in marked young. Unlike Convulsion, Aggression, although interspersed with rapid returns to the adult, was observed up to 15 m away from the parent and was not restricted to a location in front of the parent. Other young either fled from, or moved out of the path of, aggressive chicks. Adults other than the aggressing bird's parent most often moved out of the aggressing bird's path or appeared to ignore it. On 15 occasions these adults directed jabs toward the aggressing young.

The duration of Aggression given before ($\bar{x}=15.7 \pm 7.22$ s) were significantly longer ($t=2.35$, $p<.05$) than those given after feeding ($\bar{x}=13.6 \pm 7.06$ s, Fig. 8). In 86.3% ($n=271$) of observations where Aggression was occurring at the time of adult departure, it was terminated within 3 s. This proportion differed significantly from the equivalent value for Convulsion ($\chi^2=14.04$, $p<.05$).

Temporal distribution of Convulsion and Aggression

The ordering of Convulsion and Aggression in relation to feedings (Table 5) differed significantly between years ($\chi^2=42.17$, $p<.01$). This difference was a result of changes in the relative frequencies of three of the 19 identified

Fig. 8. Duration of Aggression before and after feeding.

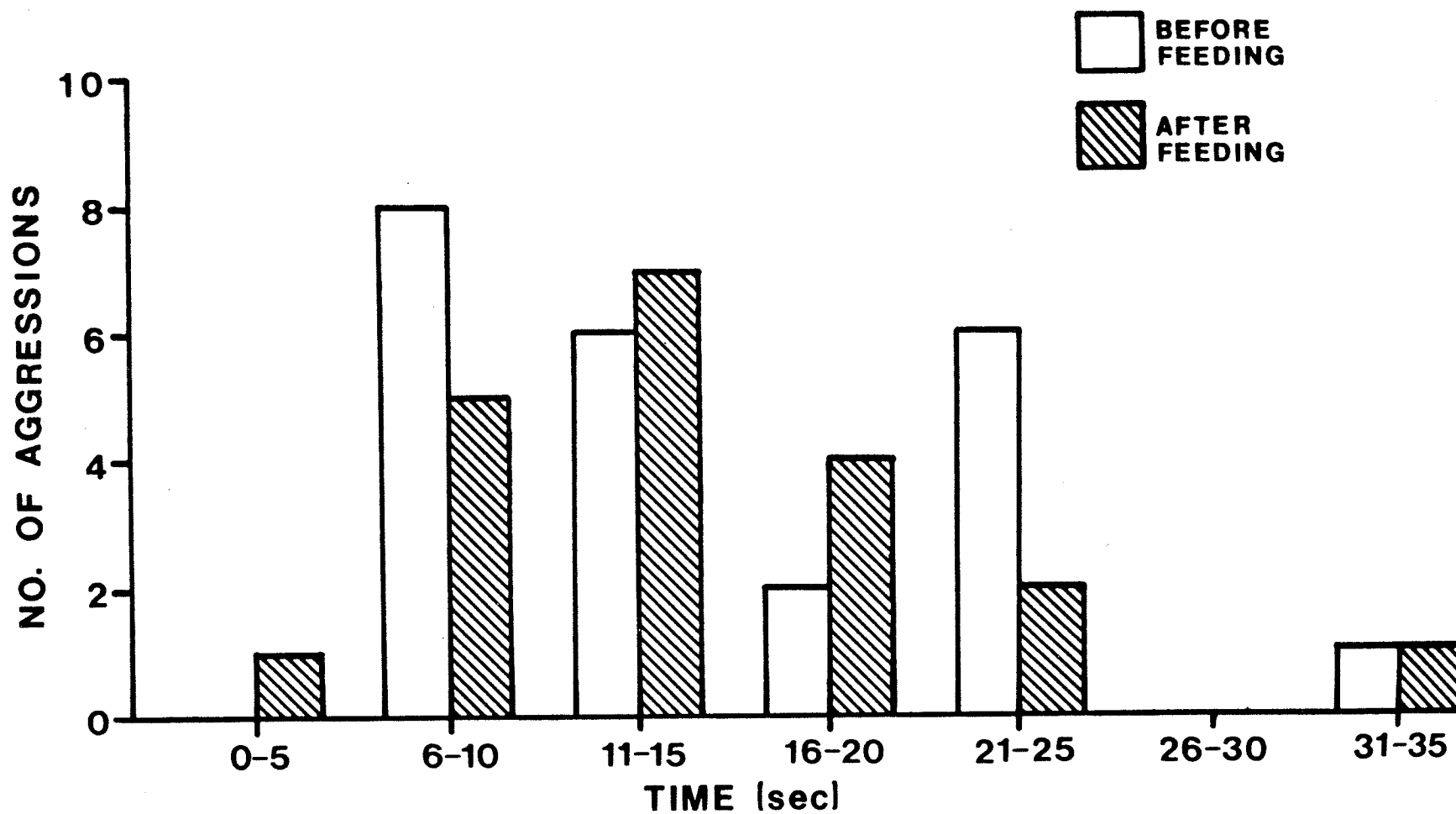


Table 5. Ordering of displays in relation to feedings.
A = aggression, C = Convulsion, F = feed

Order of displays	1982 n (%)	1983 n (%)
F	73 (12.2)	50 (9.2)
A-F	50 (8.3)	36 (6.6)
F-A	60 (10.0)	55 (10.1)
A-F-A	94 (15.1)	92 (16.9)
C-F	5 (0.8)	6 (1.1)
F-C	78 (13.3)	55 (10.1)
C-F-C ¹	2 (0.3)	2 (0.4)
A-F-C	79 (13.2)	59 (10.9)
F-C-A	58 (9.7)	50 (9.2)
F-A-C ¹	8 (1.3)	2 (0.4)
A-C-F ¹	2 (0.3)	7 (2.9)
A-F-C-A ²	45 (7.5)	73 (13.4)
A-F-A-C ²	21 (3.5)	4 (0.7)
A-C-F-A ²	4 (0.7)	19 (3.5)
A-C-F-C	7 (1.2)	14 (2.6)
C-A-F-A ¹	1 (0.2)	4 (0.7)
C-F-C-A ¹	1 (0.2)	4 (0.7)
A-C-F-C-A	10 (1.7)	13 (2.4)
A-C-F-A-C ¹	2 (0.3)	2 (0.5)
TOTAL	600	543

¹Sample sizes too small to allow between-year comparison.

²Frequency of sequence differed significantly between years.

behavioural sequences. These three sequences account for 11.67% and 17.67% of those observed in 1982 and 1983, respectively.

Analysis of behavioural sequences in which both Convulsion and Aggression occurred before or after a given feeding revealed that Convulsion bore a closer temporal relationship to the feed itself than did Aggression. Thus when both displays were given prior to a feed, Convulsion usually (96.3% of observations) followed Aggression (that is, Aggression-Convulsion-feed), whereas after a feed Convulsion usually (87.3% of observations) preceded Aggression (i.e. feed-Convulsion-Aggression, see Table 6). The frequencies and order in which Convulsion and Aggression occurred following the feed differed significantly between years ($\chi^2=19.58$, $p<.05$). In both years, however, the above pattern predominated.

Convulsion and Aggression before feeding

The frequency of Aggression prior to feeding was related to the length of the begging bout ($\chi^2=141.96$, $p<.01$, median test). Aggression was observed in only 19.9% ($n=151$) of short (<15 s) begging bouts, while 82.9% ($n=339$) of the

Table 6. Order in which Aggression and Convulsion occurred
before and after a feed for 1982 and 1983

Year	Order of displays	Displays before feeding n(%)	Displays after feeding n(%)
1982	Aggression - Convulsion	25 (96.2)	31 (21.4)
	Convulsion - Aggression	1 (3.9)	114 (78.6)
1983	Aggression - Convulsion	53 (96.4)	6 (4.1)
	Convulsion - Aggression	2 (3.6)	140 (95.9)

bouts which were longer than 15s involved Aggression (Fig 9). Similarly, Convulsion most often occurred in conjunction with longer begging bouts ($\chi^2=61.74$, $p<.01$, median test). Of 424 begging bouts which lasted less than 45 s, 2.1% involved Convulsion while 84.85% of the longer (≥ 45 s) bouts did so (Fig. 10).

Convulsion and Aggression following feeding

Most feedings ended when the adult forcefully shook the feeding young out of its esophagus. Of 1143 observed feedings, 914 (80.0%) were immediately followed by Convulsion or Aggression or both.

Table 7 summarizes the mean duration of feeds followed by Aggression or Convulsion in each year. Within each year there was no significant difference in the mean feed duration of those feedings followed by Aggression and those which were not ($t=1.33$ for 1982, $t=0.89$ for 1983, $p>.05$). The duration of feeds followed or not followed by Convulsion also did not differ significantly in either 1982 ($t=1.22$, $p>.05$) or 1983 ($t=0.21$, $p>.05$).

The amount of food delivered, but not the duration of feedings, was related to the frequency of Aggression and Convulsion. Table 8 gives the frequency of Convulsion and Aggression following feeds which involved observable disten-

Fig. 9. Frequency of Aggression with increasing duration of begging bout.
Numbers over bars indicate sample sizes.

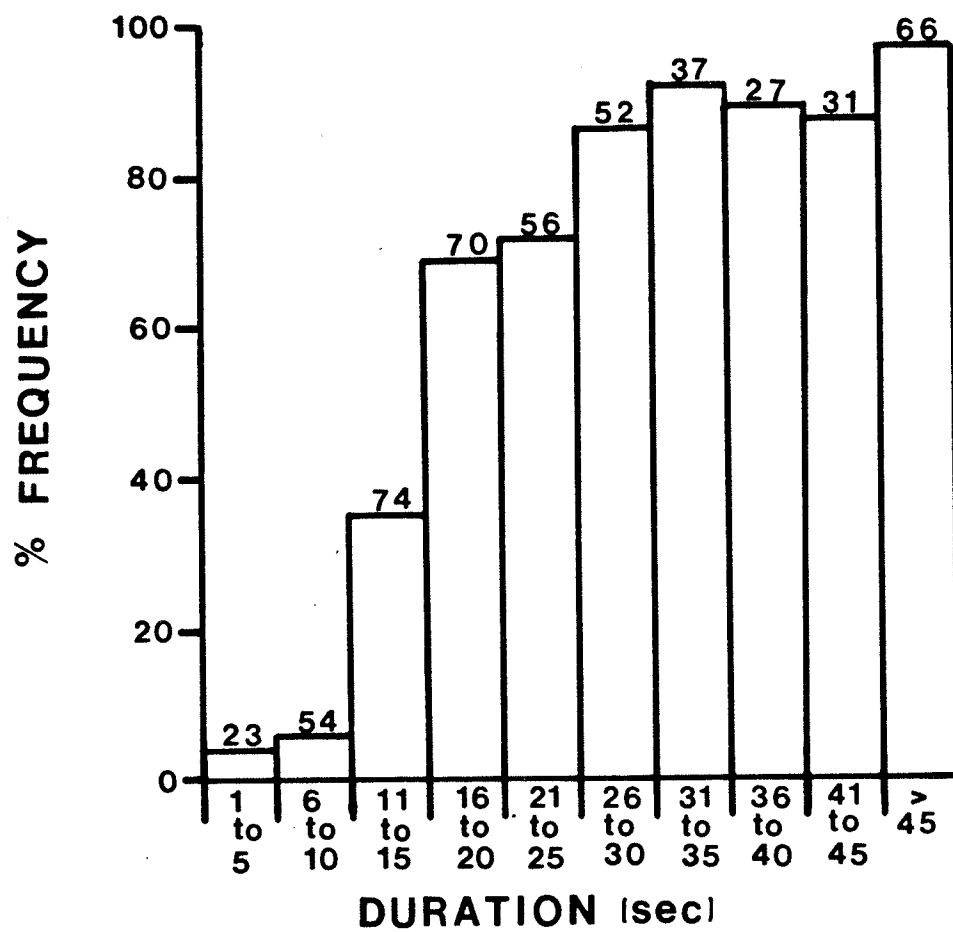


Fig. 10. Frequency of Convulsion with increasing duration of begging bout.
Numbers over bars indicate sample size.

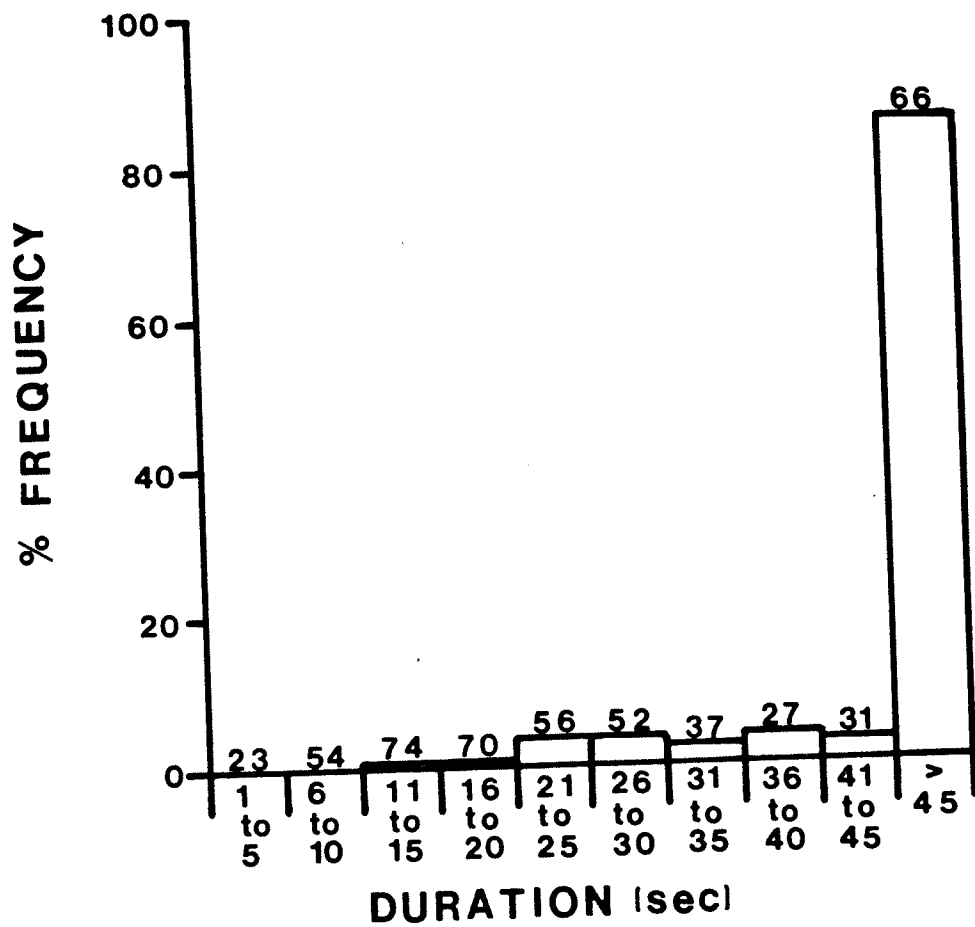


Table 7. Mean duration of feeds followed by Aggression, no Aggression, Convulsion or no Convulsion in 1982 and 1983. (Each feeding is used twice, once in relation to each display).

Year	Behaviour	Duration of feeding		
		\bar{x}	s.d.	n
1982	Aggression following feed	86.3	69.6	304
	No Aggression following feed	83.4	83.4	296
	Convulsion following feed	94.2	82.5	311
	No Convulsion following feed	86.5	70.2	289
1983	Aggression following feed	103.0	52.4	316
	No Aggression following feed	108.6	62.6	227
	Convulsion following feed	107.8	57.4	278
	No Convulsion following feed	108.0	66.4	265

Table 8. Behaviours following feeds in which the throats of chicks were or were not distended (%)

Year	Distended Throat	Display Observed following feed			
		Convulsion Only	Aggression Only	Both Convulsion and Aggression	Neither Convulsion or Aggression
1982	Present	8 (20.0)	6 (15.0)	10 (25.0)	16 (40.0)
	Absent	158 (28.2)	153 (27.3)	135 (24.1)	114 (20.4)
1983	Present	10 (12.2)	17 (20.7)	9 (10.9)	46 (56.1)
	Absent	120 (26.0)	151 (32.8)	137 (29.7)	53 (11.5)

sion of the chick's throat (i.e., the chick presumably approached satiation) and those which did not. Aggression was significantly less frequent following feeds which resulted in distension of the chick's throat in 1982 ($x^2=6.62$, $p<.02$) and in 1983 ($x^2=76.24$, $p<.01$). Convulsion was also less frequent after feeds involving throat distension in both 1982 ($x^2=5.47$, $p<.02$) and 1983 ($x^2=79.66$, $p<.01$).

Feeding Frequency

Observations from each of five pairs having one individually identifiable adult indicated that each adult returned to the colony every two days. I never observed the same adult in the colony on two or more consecutive days during the creche period.

Data collected on the total number of feeds delivered to a creche of 46 chicks support the above observations. Over a 16 day period midway through the creche stage an average of 50.0 ± 7.31 feeds were delivered each day to the 46 young.

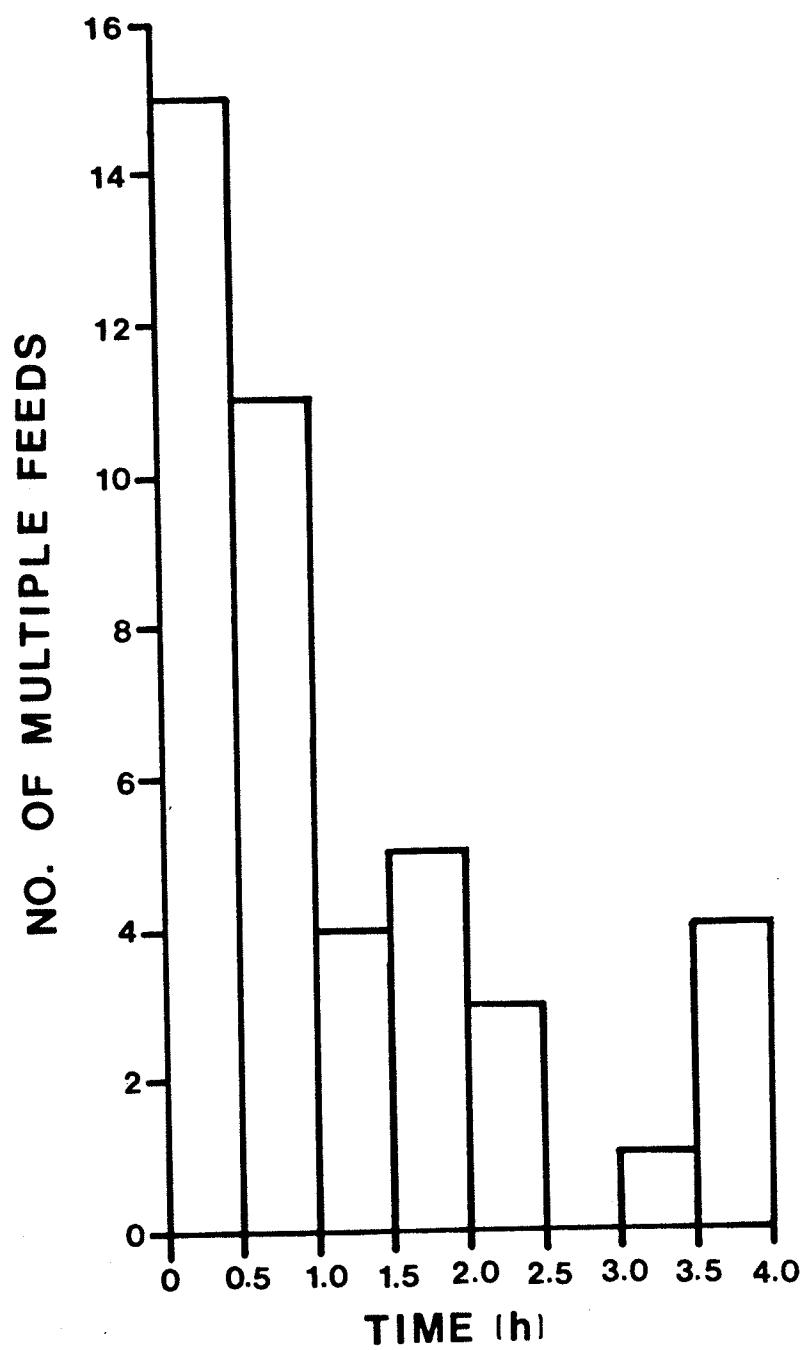
Feeding Frequency, Convulsion and Aggression in Marked Chicks

Analysis of feeds involving marked chicks indicated that young in the creche stage received an average 1.2 feedings a day (range=1 to 4, $n=298$). Multiple feedings delivered to the same chick within a single day were usually separated by

less than 2 h ($\bar{x}=1.44 \pm 1.11$ h, Fig. 11).

The frequency of Convulsion following a feed was not significantly related to the number of subsequent feeds delivered that day ($\chi^2=0.02$, $p>.05$) or to the number of feeds delivered by the presumed same parent (see above) two days later ($\chi^2=0.71$, $p>.05$). Nor was it related to the number of feeds already delivered that day ($\chi^2=0.46$, $p>.05$) or to the number delivered presumably by the same parent two days earlier ($\chi^2=0.52$, $p>.05$).

Fig. 11. Time separating multiple feeds delivered to the same colour-marked chick in a single day (n=42).



DISCUSSION

Parent-offspring Conflict

Observations suggest that Convulsion and Aggression displays are both manifestations of parent-offspring conflict (Trivers 1974), with Convulsion being an escalated form of conflict display.

Parent-offspring conflict theory (Trivers 1974) concerns the conflict which arises over the timing or amount of parental investment (Trivers 1972) directed toward each offspring. A given chick, because it is more related to itself than to its parents or siblings (present or future) may "desire" more investment than the parent is selected to provide. Thus, conflict arises because of the different optimal strategies of parent and offspring.

As Burger (1981) pointed out, parent-offspring conflict may arise over the timing as well as the amount of investment directed toward offspring. In other words, conflict could arise over either the initiation, or continuance of feeding.

Conflict Theory and Feeding-related Behaviours: A Model

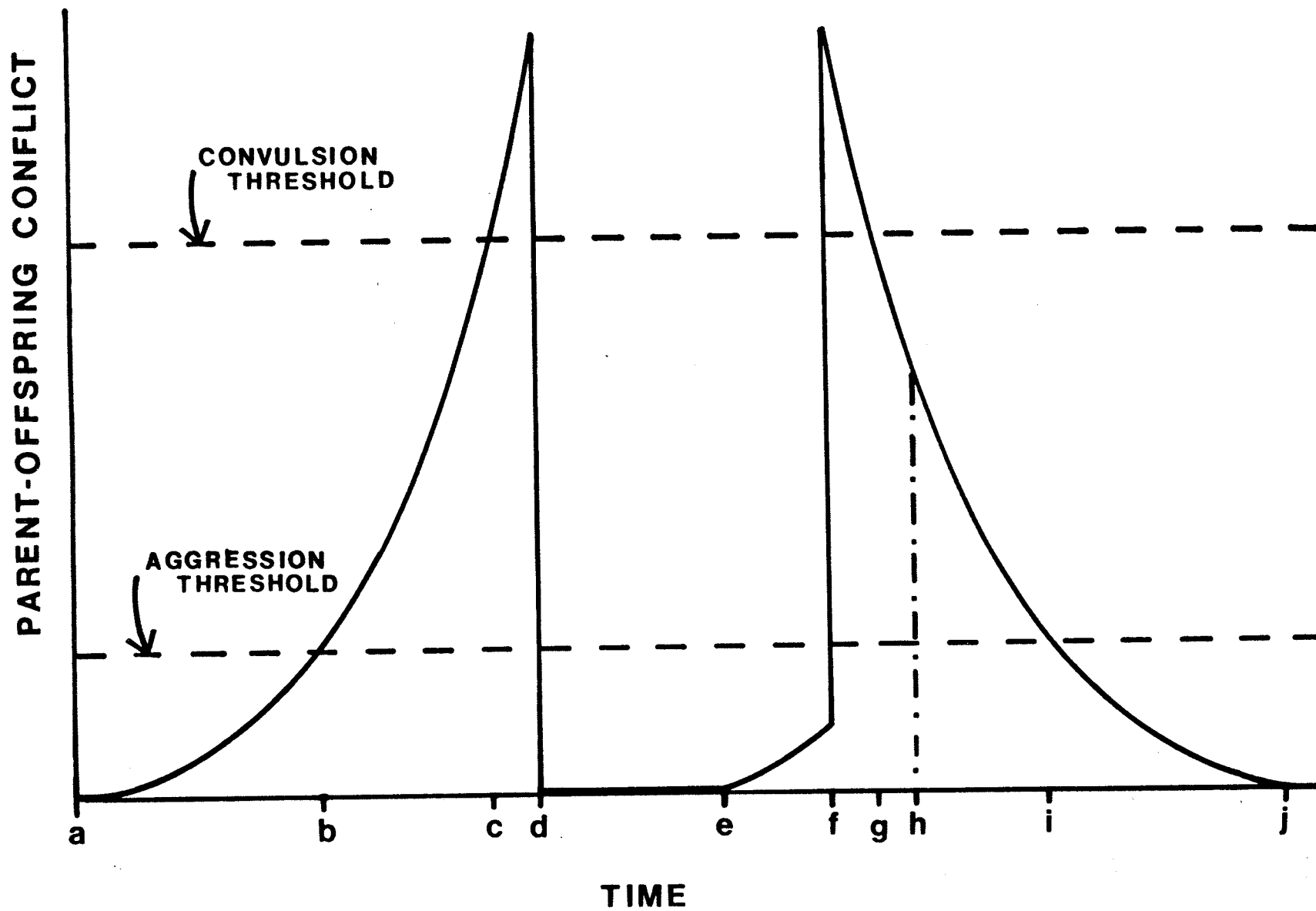
As discussed above parent-offspring conflict (Trivers 1974) is expected to arise over the amount and timing of food delivered to the young pelican during the creche stage. From the perspective of the young, it seems clear that overt behavioural manifestations of such conflict should be minimal during the time that it is actually feeding in the parent's throat. Similarly, before the parent arrives at the colony, and after the parent leaves, overt behavioural manifestation of parent-offspring conflict exhibited by the young seem unlikely to be adaptive functionally, and hence can be expected to be minimal or even non-existent. Manifestations of conflict by the young, if they indeed influence the behaviour of the parent, could be present and adaptive if they occur at any time after the arrival of the parent up to the onset of feeding, and again after the termination of feeding until the parent leaves.

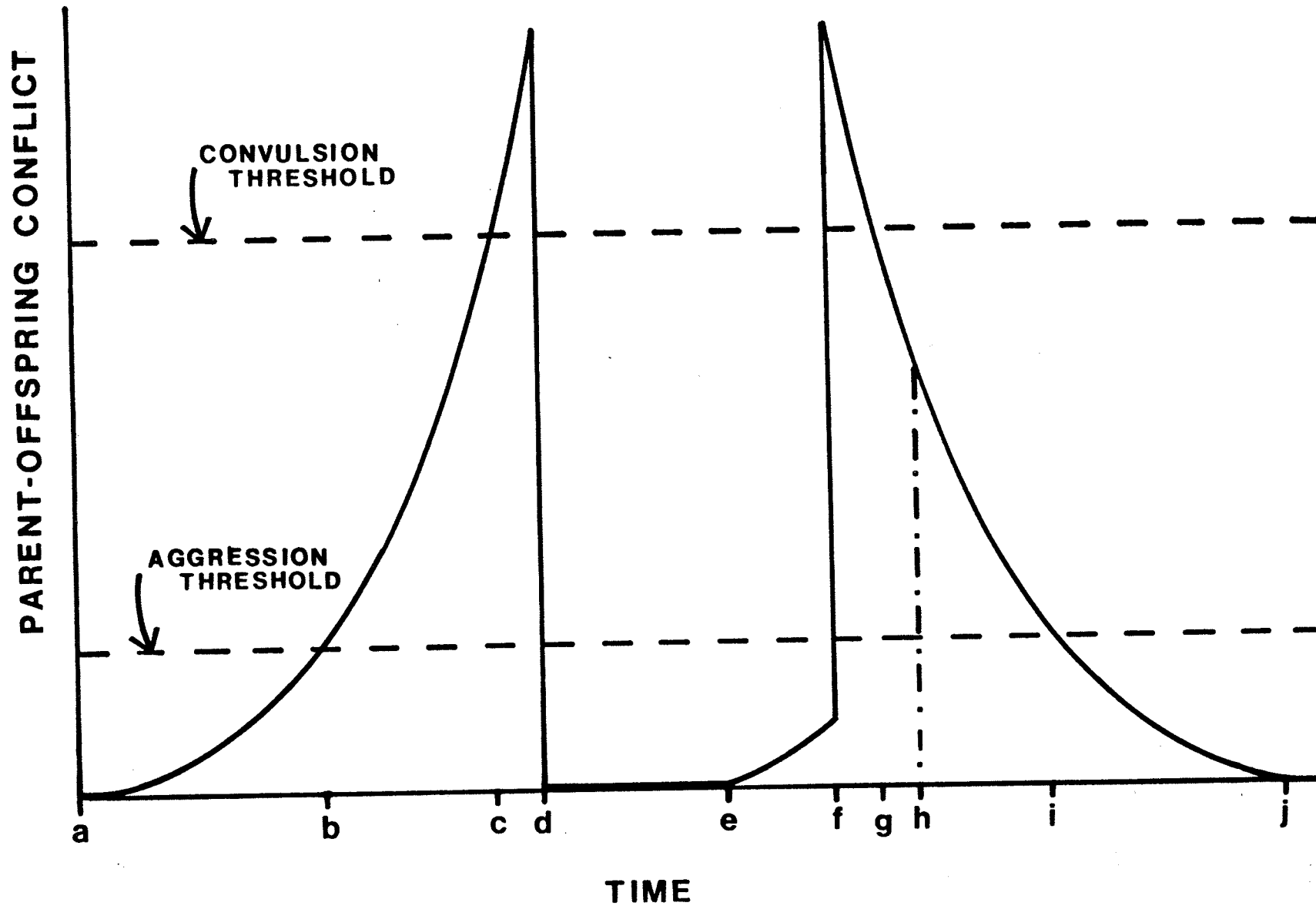
The expected level of the behavioural manifestations of parent-offspring conflict in the young is less clear than is the delineation of the period when it should occur at all. However, several considerations suggest that at least a qualitative description of expected levels of this behaviour is possible. In particular, immediately upon arrival of the parent, some time is necessarily required before a feeding can be initiated, even if the parent and young are equally willing to begin such a feeding as soon as possible. Mani-

festations of parent-offspring conflict can, therefore, be expected to be at low levels soon after the parent arrives. If the adult arrives but fails to initiate feeding almost immediately, a context of parent-offspring conflict seems to be clearly created in that the parent is failing to deliver food demanded by the young. The longer the parent fails to feed the begging young, the greater the apparent conflict created. The graphic model presented below (Fig. 12) incorporates this assumption of an increasing level of conflict as duration of the begging bout increases.

Following a feeding, creche-aged young are typically forcefully shaken out of the parents' pouch (Finley 1907; Schaller 1964; this study). The behaviour on the part of the parent strongly suggests that the parent actively terminated most feedings before the young received as much food as it would have been able to eat. The occurrence of noticeably distended esophagus in only 10.7% ($n=1143$ feedings) of young further supports this conclusion. The abrupt termination of a feeding by a parent therefore provides a context where perhaps the most intense parent-offspring conflict is likely to be manifest. These assumptions of increasing conflict levels near the termination of a feed, reaching maximal conflict levels immediately following a feed, are incorporated into the model presented in Fig. 12. It is further assumed in the model that the intensity of conflict would subsequently wane over the time the parent

Fig. 12. The expected levels of overt manifestations of parent-offspring conflict over time, before, during and after a feed. At point "a" the adult has just returned to the colony. Conflict is low but intensifies over time until the Aggression ("b") and eventually Convulsion ("c") thresholds are reached. Convulsion is quickly followed by feeding and a drop to low or negligible conflict levels ("d-e"). Late in the feed ("e-f") conflict once again intensifies as the young is shaken out of the parental throat. At the termination of feeding, conflict rapidly intensifies to surpass the Convulsion threshold ("f"). As conflict wanes the chick switches back to Aggression ("g"). Conflict continues to wane and falls below the Aggression threshold ("i"). Finally conflict drops to low or negligible levels ("j"). Should the adult leave while conflict is still high all displays are abruptly terminated ("h").





remains in the colony after a feeding (Fig. 12), possibly as a joint result of increased distance between parent and young as the adult moves away from the chick after a feeding, plus the apparent high energetic cost to the young of continued high levels of activity.

The model presented in Fig. 12, which incorporates the main assumptions described above, illustrates qualitatively the expected levels of overt manifestations of parent-young conflict over time, before, during and after a feed. Superimposed on the curve of conflict level are two horizontal lines depicting presumed thresholds of conflict for producing Aggression and Convulsion, the latter threshold being higher than the former. These hypothetical thresholds were not measured directly, but rather were postulated to permit predictions as to the timing of the various behaviours exhibited by the young at the time of feeding. A summary of these predictions from the model and their relevance to observed results, follows. Early in the begging bout (<15s, see Fig. 9) conflict over the onset of feeding is assumed to be low, as shown by the model in Fig. 12. The chick, at this time, should display low-intensity begging, as indeed it does. This is manifested by running its bill along the adult's tomtia (see Schaller 1964). As begging continues (>15s, Fig. 9), conflict intensifies, the Aggression threshold is reached, and the young begins Aggression directed at other chicks, interspersed with rapid returns to the adult.

Finally, if the begging bout exceeds 45s (see Fig. 10) the Convulsion threshold is reached. At this point conflict is intense and Convulsion begins, normally to be followed rapidly by the initiation of feeding, when conflict levels become negligible.

Near the end of a feeding, conflict once again intensifies as the adult begins to shake the young out of the pouch. Overt behavioural manifestations of conflict are not expected at this point since, even if the Aggression or Convulsion threshold is reached, the chick has no opportunity to display while still in its parent's esophagus. Immediately following the termination of feeding, conflict intensity would presumably depend on the amount of food delivered to the chick. If the chick was still hungry, as it evidently was at the termination of most feeds, the Convulsion threshold is again surpassed and the young begins Convulsion. As conflict intensity then declines the chick switches back to Aggression. Finally, when the parent leaves the area overt conflict ceases, and Convulsion or Aggression is terminated, typically within 3s of adult departure. The fact that Convulsion is more likely to be terminated within 3s of adult departure (96.7% of observations) than is Aggression (86.3% of observations) is consistent with the hypothesis that Convulsion, as a more intense and energetically expensive display, depends more on the proximity of the adult.

The predominant ordering of feeding-related behaviours (mild begging-Aggression-Convulsion-feeding-Convulsion-Aggression) is in agreement with, and indeed initially suggested, the above model and interpretations. Given that the periods immediately prior to and following feeding are those involving the most intense conflict, as they would intuitively seem to be, Convulsion as a manifestation of high conflict levels is predicted to more often occur immediately before or after a feeding than is Aggression when both occur before or after the same feeding. The results of both 1982 and 1983 (Table 6) strongly support this prediction. An identical ordering of displays was also noted at the East Shoal Lake colony in 1981 (R. M. Evans pers. comm.).

Several other aspects of the data collected can also be explained in the context of parent-offspring conflict. The infrequency of Convulsion prior to feeding is of particular interest since one might expect begging displays to be most commonly used at that time. The key element here appears to be the behaviour of the adults. Round-trip flights from East Shoal Lake to the foraging grounds range from 80-160 km (O'Malley and Evans 1982a), and in some colonies may be as much as 600 km (Johnson and Sloan 1978). Given the distances adults must travel it seems likely that returning parents are willing to initiate feeding quickly. Thus conflict would not escalate to the Convulsion threshold before most feedings (Figs. 10, 12). However, when begging bouts become

more extended the chick's desire to be fed and the parent's apparent reluctance to deliver food provide a basis for increasing conflict, eventually reaching the threshold for Convulsion which was seen in 84.8% of all feeds involving extended (>45s) begging bouts.

As mentioned above, the intensity of conflict following the feed is expected to depend on the amount of food delivered to the chick. Chicks which approached or reached satiation (as measured by throat distension) are therefore expected to have exhibited lower frequencies of Convulsion and Aggression than those which did not. Results comparing the relative frequencies of displays in these two groups (Table 8) are consistent with the prediction.

Functional Significance of Convulsion and Aggression

Begging (though not directly in the conflict context) has been proposed previously as the major function of both Convulsion and Aggression in white pelicans (Behle 1958; Schaller 1964) and in pink-backed pelicans (Burke and Brown 1970; Din and Eltrengam 1974). The results of the present study revealed Convulsion and Aggression are closely associated temporally with both low-intensity begging and the act of feeding, and therefore, support the above interpretation.

Aggression, because it is directed toward conspecific chicks and, in most cases, serves to clear an area around

the adult, may also act in defense of the food source, in this case the returning adult. Young other than the returning parent's own offspring commonly left the creche to approach an incoming adult (see also Evans 1984a). Aggression may serve to disperse these potential competitors from the area around the parent, thus ensuring the aggressing chick sole access to the food delivered. Such a strategy would be particularly important in broods which were not reduced in size (see Knopf 1979). If both siblings were reared to the creche stage and if, thereafter, each parent returned to the colony only once every two days, as at East Shoal Lake, one would predict intense competition between siblings over access to the parent. Even in colonies in which adults might return more often, sibling competition would still be expected.

It is important to note that begging and defense of food source are not mutually exclusive functions of Aggression. Given that both siblings seldom survive to the creche period and that parent-young recognition would appear well developed by this stage (Schaller 1964; this study) defense of the parent as a food source may not be critical. Aggression may, in these cases, also serve to direct the attention of the parent toward the young while at the same time clearing the area of potential nonsiblings competitors. Further investigation is required before the importance of each of these functional explanations of Aggression can be determined.

The functional significance of Convulsion and Aggression following the feeding is not clear. If displays given following a feed act as begging displays, then they would not appear very effective, in that the number of subsequent feeds delivered in the same day or by the presumed same parent upon its return to the colony two days later was not affected. Nor would they seem to affect the timing of the next feed, since a given adult is not likely to return to the colony until near midday (O'Malley and Evans 1982) approximately 48 h after delivering a feed (this study) regardless of the displays given by its chick.

Displays following the feed could, however, still influence the amount of food delivered on the next colony visit. Unfortunately it was not possible to test this hypothesis with the available data. Whatever its functional significance, the evidence strongly points to Convulsion and Aggression following the feed as manifestations of parent-offspring conflict over the continuance of the feed.

Alternative explanations concerning the functional significance of Convulsion are not generally supported by the data collected in this study. Chapman (in Bent 1964) in a study of brown pelicans and Vestjens (1977) working on the Australian pelican suggested Convulsion is a result of oxygen deprivation incurred while feeding in the parental esophagus. If Convulsion was a physiological response to low oxygen levels then it should not be observed before feeding

and its frequency should increase with increasing feed duration. Neither of these predictions are verified by the data. Convulsion was observed before 7.1% of the feeds and its frequency did not relate to the duration of the feed (Table 7). Convulsions before feeds and a lack of any relationship to the duration of feeds was also noted at this colony in 1981 (R.M. Evans pers. comm).

Schaller (1964) has suggested that in white pelicans Convulsion serves not only as a begging display but also as a means by which the chick inhibits attack tendencies in the adult and as a mechanism which facilitates parent-offspring recognition. If displays functioned in parent-offspring recognition then it can be predicted that they would more commonly occur prior to or during the early stages of parent-young reunion. The low frequency of Convulsion prior to the feed and its restriction to a period after the young had obviously begun to beg from the presumed parent, are not consistent with this prediction. I never observed aggression by an adult directed toward its presumed offspring, suggesting little if any functional need for a display that inhibits or suppresses parental aggression.

Finally the occurrence of Convulsion before feeds, and the observed low frequencies of Convulsion after those feeds in which the chicks' throat became distended do not support Chapman's (in Bent 1964) contention that the display aids in swallowing.

SUMMARY

Aggressive behaviours occurring in association with about 90% of all feedings developed in chicks approximately three weeks old. These behaviours involved aggression directed toward self (Convulsion) or other young (Aggression).

Observation of feedings revealed that: (1) when both Convulsion and Aggression occurred before or after a given feeding, convulsion bore a closer temporal relationship to the feed itself than did Aggression, (2) the frequency of both Aggression and Convulsion prior to feeding increased as the length of the begging bout increased, (3) the frequency of Convulsion and Aggression following feeding was not related to the duration of the feed but did depend on the amount fed (as measured by throat distension).

Observations of identifiable parents and chicks revealed that most chicks receive a single feeding each day, each parent returning to the colony every two days. The frequency of multiple feeds given to the same chick on the same day or (by the presumed same parent) two days later was not related to the frequency of Aggression or Convulsion given after a feeding.

A model is proposed to explain Aggression and Convulsion as manifestations of parent-offspring conflict over the initiation or continuance of feeding. The close association of these displays with both feeding and low-intensity begging suggests that they function primarily as begging displays or, for Aggression, to drive other young away from the parent food source. Alternative functions of Convulsion and Aggression are not supported by data collected in this study.

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