

# TEMPORAL PATTERNS IN PRE-FLEDGLING SURVIVAL AND BROOD REDUCTION IN AN OSPREY COLONY<sup>1</sup>

JOHN M. HAGAN

Department of Zoology, North Carolina State University, Raleigh, NC 27695

**Abstract.** Temporal patterns in pre-fledgling mortality were examined in a coastal North Carolina Osprey (*Pandion haliaetus*) colony by checking nests weekly throughout two breeding seasons. Individuals experienced high weekly survival during incubation (>90%), but exhibited a dramatic drop in survival at two to three weeks after hatching. The mortality pattern was identical in both years of study and was characteristic of both early and late nesters. This mortality appeared related to food-stress and occurred when nestlings entered the steep phase of logistic growth. Survival data were also used to test O'Conner's brood reduction model. The model predicted that brood reduction should occur in the population and should be manifested as fratricide, rather than infanticide or suicide. Nestling behavior was in accordance with the prediction of the model in that sibling aggression was common, but parents appeared to feed whichever nestling begged most vigorously. The calculations suggested that this population barely exceeds the threshold for fratricide, an interesting result considering the facultative nature of brood reduction in Ospreys.

**Key words:** Brood reduction; Osprey; fratricide; behavior; food-stress; mortality.

## INTRODUCTION

Brood reduction refers to a presumed adaptive process that leads to a sequential decrease in the number of nestlings in a nest. A necessary precursor to brood reduction is hatching asynchrony. Lack (1954) reasoned that asynchrony could impart a survival advantage to the individual(s) that hatched first under limited-food conditions. The larger, first-hatched nestling exhibits dominance over younger, weaker siblings, thus inhibiting their access to food provisioned by the parents. Lack proposed that this aggression leads to the survival of a portion of the brood rather than to the demise of all. The cost of producing young that are doomed when food is scarce is presumably more than compensated for by the successful raising of the extra young when food is abundant. Species in which brood reduction in food-limited conditions has been reported include South Polar Skuas (*Catharacta maccormicki*, Procter 1975), Goshawks (*Accipiter gentilis*, Schnell 1958), Hen Harriers (*Circus cyaneus*, Watson 1977), Swainson's Hawks (*Buteo swainsoni*, Bechard 1983), Ospreys (*Pandion haliaetus*, Poole 1982), Herring Gulls (*Larus argentatus*, Parsons 1975), Tawny Owls (*Strix aluco*, Southern 1970), and Curve-billed Thrashers (*Toxostoma curvirostre*, Ricklefs 1965).

Theoretical models of the evolution of brood reduction have been presented by Stinson (1979) and O'Conner (1978). O'Conner's model uses the probability of survival of the largest brood (of size B) compared to the probability of survival of a smaller brood (B-1), in

conjunction with the relatedness of family members involved, to predict whether brood reduction would increase the inclusive fitness of those members. Brood reduction might occur in three ways. First, one or more nestlings may inhibit the youngest nestling from feeding through aggression, thus leading to its starvation (fratricide). Second, a parent may selectively feed individuals at the expense of the nestling with the least probability of surviving (infanticide). And finally, based strictly on an inclusive fitness argument, the youngest or weakest nestling may voluntarily opt to discontinue eating, thus leading to a greater probability of its sibling's survival and a concomitant increase in its own inclusive fitness (suicide) (O'Conner 1978).

This model involves the interests of three different types of individuals: the parents, the surviving siblings, and the victim. Each has its own interests, and they are often in conflict. According to the model, whose interests prevail and thus which mechanism accomplishes the brood reduction depends on the differential in probability of survival of a member of the largest brood (size B) vs. the probability of survival of a member of a brood that begins at size B-1. The larger this differential, the greater the gain of eliminating a nestling competitor. A comparison of the three differential thresholds necessary for manifestation of brood reduction behaviors shows that the threshold is always smallest for survivors and largest for victims. Thus, when the survival differential threshold is achieved, fratricide will be the first mechanism to appear, followed by infanticide and finally suicide, with increasing survival differentials.

There have been no attempts to test O'Conner's model other than his own. In this paper,

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TABLE 1. Reproductive summary of the Lake Ellis Simon Osprey colony. Numbers indicate mean values. Sample sizes and standard deviations, respectively, are presented in parentheses.

	Year		Prob > <i>t</i> †
	1983	1984	
Clutch size	2.54 (41,0.554)	2.76 (41,0.289)	0.130
Brood size*	2.34 (29,0.814)	2.35 (31,0.661)	0.958
Fledglings/active nest	0.93 (41,0.848)	1.02 (41,0.961)	0.625

\* At the week of hatching, and including only those nests which reached the nestling stage.

† Student's *t*, probability that observed differences were due to chance.

I compare the model's predictions with observed temporal trends in nestling mortality in a colony of Ospreys (*Pandion haliaetus*) in coastal North Carolina. Also, the model's prediction of which mechanism is expected to accomplish the brood reduction (fratricide, infanticide, or suicide) is compared to observed behaviors.

### STUDY AREA AND METHODS

A particularly dense Osprey population occurs at Lake Ellis Simon (LES), a privately owned freshwater lake in coastal North Carolina (Craven Co., 35°50'40"N, 76°59'06"W). LES occupies about 600 ha and its water depth averages about 1.3 m. It is characterized by an abundance of emergent aquatic vegetation and cypress trees (*Taxodium* spp.). All Osprey nests were individually identified, and occur in live, emergent cypress.

Fifty to fifty-five pairs inhabit LES each breeding season, although not all breed. Nearest-neighbor distances between occupied nests ranged between 100 and 450 m; when distances were classified into 50 m divisions, the modal distance fell in the 151 to 200 m category.

Because the population is localized, the productivity of each individual nest was easily monitored. Often an accurate assessment of age-related mortality of nestlings is difficult to accomplish because some nests are discovered long after they have been initiated (Mayfield 1975). However, the necessary data are easily obtained from colonially breeding species, such as Ospreys, for which nesting occurs in a restricted and predictable location. Ospreys return to the lake from their wintering grounds in late February and early March. During the 1983 and 1984 breeding seasons, each nest in the colony was checked weekly for the presence of eggs or nestlings, beginning in late March before egg laying commenced, and continuing until all nestlings had fledged. Because nests in the colony ranged in height from 1 m to 9 m above water level, checking nests was easily accomplished using a 4.3 m aluminum jon boat and a mirror attached to the end of a telescoping aluminum pole. Proximity of the nests to one another allowed all nests in the popu-

lation to be checked in one to two hr, depending on weather conditions. Each nest usually could be checked in less than one min, and the parents were seldom displaced from the nest for more than about two min.

For Ospreys, eggs are laid at two or three day intervals, with consistent incubation beginning with the second egg (Poole 1982). Thus, the ages of nestlings within a nest are likely to be several days different. However, because nests were checked on a weekly basis, the best "average age" of the clutch or brood is used to represent the age of any member of that nest (i.e., 1.5, 2.5, 3.5 weeks, etc.).

### RESULTS

#### PRE-FLEDGLING SURVIVAL

The productivity of the population was remarkably similar for the two years. In 1983 and 1984, 109 and 114 eggs were laid, respectively. Each year, 41 nests produced at least one egg (active nest). There were no significant differences between years in clutch size, number of nestlings per active nest, or number of fledglings per active nest (Table 1).

Using data from the weekly nest checks, I constructed a pre-fledgling "life table" using weeks as age class intervals (Table 2). The interval from the day an egg is laid to the day of fledging is about 13.5 weeks in Ospreys. Eggs hatch at about five weeks of age and nestlings fledge at seven to eight weeks of post-hatching age. The age class intervals of the life table represent the age of individuals relative to their own laying date rather than to time of season. Thus, I assume that these patterns of mortality reflect age and not some correlate of absolute time. I also assume that no eggs were laid and then disappeared in less than the time between nest checks (one week).

All eggs which exceeded 5.5 weeks without hatching subsequently disappeared. These eggs were assumed to be inviable and were not included in the calculations. In 1983 there were 17 such eggs, and in 1984 there were 24 (18.4% of all eggs). However, those eggs which disappeared between pre-fledgling age 5.5 and 6.5 weeks could have influenced the nestling weekly survival rate at pre-fledgling age 4.5. That

TABLE 2. "Life-table" of pre-fledgling Ospreys in the Lake Ellis Simon colony. Data from the 1983 and 1984 field seasons have been combined.

Nesting age (wks)	Pre-fldg age (wks)	Deaths* D	$f_t$ †	$l_t$ ‡	$P_x$ § ± 1 SD
—	0	0	182	—	—
—	0.5	1 (1)	181	0.995	0.939 ± 0.018
—	1.5	11 (2)	170	0.934	0.929 ± 0.020
—	2.5	12 (2)	158	0.868	0.975 ± 0.012
—	3.5	4 (2)	154	0.846	0.968 ± 0.014
—	4.5	5 (5)	149	0.819	0.940 ± 0.020
0.5	5.5	9¶ (5)	140	0.769	0.950 ± 0.018
1.5	6.5	7 (4)	133	0.731	0.902 ± 0.026
2.5	7.5	13 (8)	120	0.659	0.792 ± 0.037
3.5	8.5	25 (16)	95	0.522	0.895 ± 0.031
4.5	9.5	10 (9)	85	0.467	0.965 ± 0.020
5.5	10.5	3 (3)	82	0.451	0.963 ± 0.021
6.5	11.5	3 (3)	79	0.434	1.000
7.5	12.5	0	79	0.434	1.000
8.5	13.5	0	79	0.434	1.000

\* Numbers in parentheses indicate the number of nestlings not involved in whole clutch or brood losses.

† Number of individuals remaining alive at indicated age interval.

‡ Proportion of original cohort remaining alive.

§ Probability an individual will live one more week.

|| Standard deviation for a binomial probability.

¶ Could have been egg or nestling deaths.

is, if an egg hatched one week late (between 5.5 and 6.5 weeks of age) and the resulting nestling subsequently disappeared before the next nest check, it would have been recorded as an inviable egg, rather than a 0.5-week nestling death, and eliminated from the table. Six eggs disappeared between pre-fledgling age 5.5 and 6.5 in 1983, and 11 in 1984 (7.6% of all eggs). Thus, the pre-fledgling survival for the transition from egg to nestling (pre-fledgling age 4.5 to 5.5) could have been overestimated. Survival rates for all other ages are accurate because every nest in the population was included in the sample, and it is very unlikely that a viable egg would have reached age 6.5 weeks without hatching.

The most informative column of the life table is the one which reports weekly probabilities of survival ( $P_x$ ). These values were very similar for the two years (Fig. 1). During the incubation stage, eggs had a high probability of survival; their weekly survival rates never dropped below 0.90. During the nestling period, there was a dramatic drop in survival rate at nestling age 2.5 (Table 2). That is, a nestling at age 2.5 wks had a relatively low probability of living one more week. That the pattern of mortality was so similar for the two years suggests that the observed drop in survival reported in Table 2 was not likely to be caused by some coincidental catastrophe like a storm.

To further examine the possible influence of undetected meteorological events which may have contributed to the pattern of mortality, I constructed separate life tables for early and late nesters. In this case, data were pooled from

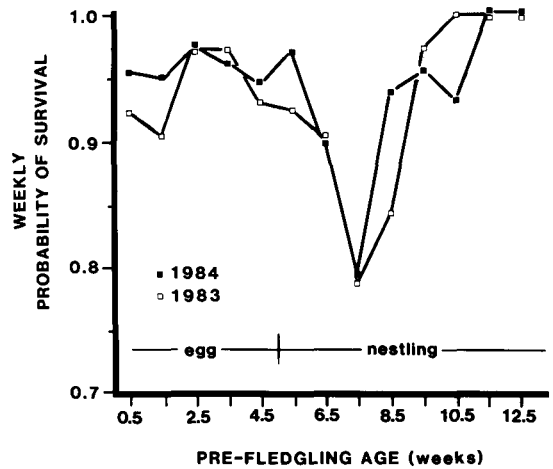


FIGURE 1. Weekly pre-fledgling survival rates of Ospreys at Lake Ellis Simon for 1983 and 1984, separately.

the two years. Nests which contained nestlings during the first three weeks of the nestling period (as defined by the first egg to hatch) were considered early nesters ( $n = 34$ ), and the rest as late nesters ( $n = 48$ ). There was a substantial drop in survival at post-hatching age 2.5 weeks in both groups, although late nesters realized the most dramatic drop in survival a week earlier than the early nesters (Fig. 2). Nevertheless, it is unlikely that such similar patterns of mortality would have emerged in both groups had the dip in survival reported in the pooled data (Table 2) been a function of some coincidental event. Rather, it seems intrinsic to this population's reproduction.

To compare timing of mortality with growth of nestling Ospreys, I constructed a logistic growth curve for nestlings (Ricklefs 1968) based on a growth rate constant determined by Stinson (1977) for Ospreys in the Chesapeake Bay (Fig. 3). The sudden drop in survival occurred at the age when nestlings begin to grow rapidly. The probability of surviving to the next week is lowest at the age 2.5 weeks when the upcoming week is characterized by near maximum growth rate. In both years it was not uncommon to find intact dead nestlings at 3.5 weeks after hatching, suggesting that starvation was the cause of this mortality.

Of the 13 nestling deaths between age 1.5 and 2.5 (see Table 2), 5 of these (38%) were involved in whole brood losses. Of the 25 deaths which occurred between age 2.5 and 3.5 weeks, 9 (36%) were related to whole brood losses. The remaining 17 were losses of single nestlings from broods of 2 or 3. The loss of whole broods at these age classes indicates that brood reduction cannot be the sole function of observed mortality. Nevertheless, even with removal of nestlings involved in whole-brood losses from the life table, a noticeable increase

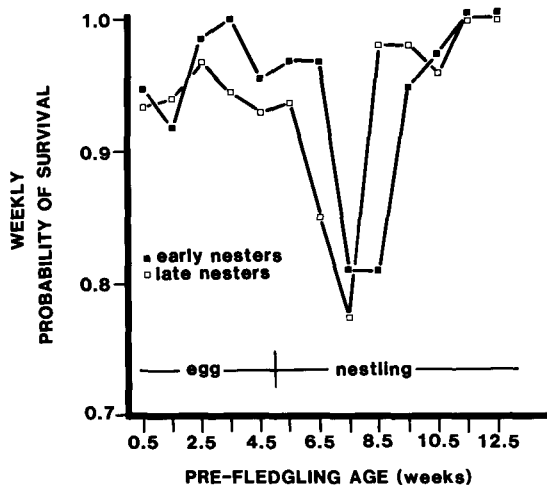


FIGURE 2. Weekly pre-fledgling survival rates of Ospreys at Lake Ellis Simon separated into early nesters and late nesters. Data are pooled from both years of study.

in mortality remains evident at nestling age 2.5 weeks (see Table 2).

Further evidence that brood reduction did play a role in nestling mortality was provided by mean duration of intact, 3-nestling nests, before a death was encountered. If 7.5 weeks is used as the maximum age a nestling can reach (fledging age), the mean life expectancy of a 3-nestling nest is 3.8 weeks ( $n = 30, SE = 0.31$ ), while that of a 2-nestling nest is 5.5 weeks ( $n = 21, SE = 0.52$ ). Thus, a 3-nestling nest had a significantly shorter life expectancy ( $P = 0.02$ , Wilcoxon two-sample test). Interestingly, the life expectancy of a 2-nestling nest resulting from a 3-nestling nest (5.5 weeks) was the same as that of an original 2-nestling nest. That is, the first death in a 2-nestling nest occurred at the same time as the second death in a 3-nestling nest. Of the 30 nests which started the nestling period with broods of 3 young in the two years of study, the entire brood fledged for only 3 of those nests (10%). In contrast, of 21 2-nestling nests, both nestlings successfully fledged on 11 nests (52%). Of the 30 3-nestling nests, at least 2 nestlings fledged from 14 of them (47%).

TEST OF O'CONNOR'S MODEL

The data collected on nestling survival at Lake Ellis Simon allowed a test of O'Connor's model, specifically its prediction of which process of brood reduction, if any, should occur. For nests that started out as 3-nestling nests (B), the probability that any member of that brood would survive to fledging was 0.488. For 2-nestling nests (B-1), the probability of surviving to fledging was 0.666 (Table 3). Using O'Connor's method of calculating differential in mortality of these two nest types, I con-

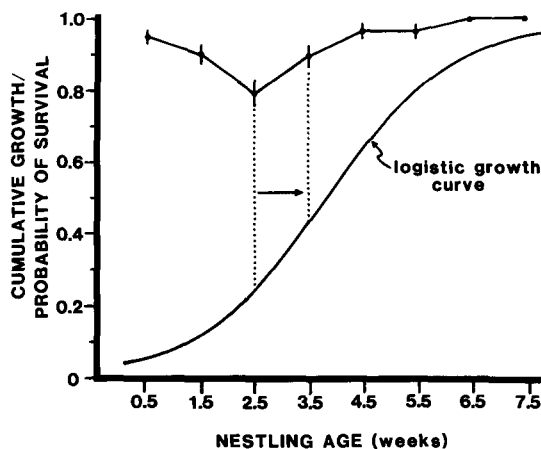


FIGURE 3. Logistic growth curve of a nestling Osprey (represented as proportion of fledging weight) overlaid on nestling weekly probabilities of survival. Vertical bars on survival probabilities indicate  $\pm 1 SD$ . Survival probabilities represent pooled data from both years of study. The week of lowest survival is projected downward to the growth curve for comparison.

verted the probabilities to daily mortality rates, and subtracted the larger from the smaller. The daily mortality differential expressed as a percent is then 0.574. The model predicts that in order for the victim of the brood reduction to voluntarily opt for his own death, a differential of at least 1.28% is necessary. For infanticide to occur, a differential of 0.75% is required. The differential required for fratricide to evolve is 0.53%. The observed differential of 0.57% is sufficient for fratricide, although barely so.

Though quantitative data on sibling aggressive behavior were not taken, qualitative observations during time-budget observations on parent birds in 1983 indicated that sibling aggression was common. Larger nestlings tended to position themselves between the parent and smaller nestmates during feeding bouts. If smaller birds attempted to beg before the larger was satiated, vigorous blows to the head and neck of the younger bird usually ensued. Parent birds would not reposition themselves in favor of the subordinate nestling. Rather, it appeared that they fed whichever nestling was the closest to the food item, suggesting the absence of infanticide behaviors.

TABLE 3. Seasonal survival probabilities and corresponding daily mortality rates for nestlings from 3-nestling nests and nestlings from 2-nestling nests.

Brood size	# Fledged/ # hatched	Probability of surviving to fledging	Daily mortality rate (%)
3	44/90	0.488	1.32
2	28/42	0.666	0.75
Observed daily mortality differential (%) = 0.57			

## DISCUSSION

### PATTERNS OF MORTALITY

It seems that nestling Ospreys at LES reach a survival bottleneck at two or three weeks after hatching. Because a similar pattern was observed for early and late nesters and in both years, brood reduction is a likely explanation of the patterns. Assuming that brood reduction is a manifestation of food supply, its occurrence at two or three weeks of nestling age at LES suggests that food is being supplied at levels far below that necessary to raise a 3-nestling nest. This is supported by the uncommon occurrence of a 3-nestling nest surviving to fledging, and the fact that once brood reduction occurred in 3-nestling nests, the resulting nestlings had the same life expectancy as those of 2-nestling nests.

Certainly other sources of mortality besides brood reduction are contributing to the death of nestling Ospreys at LES. Potential predators at LES could include Fish Crows (*Corvus ossifragus*), Brown Water snakes (*Nerodia taxispilota*), and Great Horned Owls (*Bubo virginianus*). Predation by these sources has never been witnessed, but given the size of the female and her vigilance at the nest, only predation by Great Horned Owls seems plausible. Regardless of the source or quantity of predation, it would not be expected to consistently select disproportionately for two- to three-week-old nestlings, throughout the entire breeding season.

Given the exposure of nests over open water, severe weather could be an important source of nestling mortality. Winds sometimes become extreme and can blow down an entire nest, although only one nest blew down during the nestling period in the two years of study. Severe winds associated with thunderstorms are common at LES during the nestling period and may account for some whole brood losses observed.

Such catastrophic events are not likely to play a role in controlling the onset of brood reduction, but weather could be important indirectly. The amount of food a male can catch may be weather-dependent (Grubb 1977). Fish are difficult to spot from the air when rain or wind disrupts surface water, and decreased provisioning by the male during extensive periods of such conditions will increase hunger of nestlings and promote brood reduction behaviors.

Brood reduction is commonly associated with low food abundance, but at LES brood reduction may be more a function of the geometric position of the colony site relative to the foraging grounds. The lake is located about 13

to 14 km from three estuarine bodies of water, each in different directions, all of which serve as primary sources of food for the colony. Males supply nearly all of the food for the family and exploit schooling estuarine fish at these areas, rather than freshwater fish in the lake itself. To supply food to the brood, males therefore flew round trip distances of at least 26 km up to four times a day. Although representing a great deal of effort on the part of the male, this rate is low when compared to fish delivery rates reported in other studies of Ospreys (Green 1976; Stinson 1978; Levenson 1979; Jamieson et al. 1982a, b; Poole 1982; Van Daele and Van Daele 1982). While food may be plentiful at its source, getting adequate quantities to the young may be difficult. Thus, factors other than fluctuations in food abundance, such as distance from colony site to foraging areas, may play a critical role in the evolution of brood reduction. For such populations, the manifestation of brood reduction may be relatively constant year to year, while remaining facultative for the species as a whole.

### MECHANISM OF BROOD REDUCTION

The differential in survival of nestlings in 3- and 2-nestling nests at LES barely exceeds the threshold necessary for sibling aggression to evolve according to O'Conner's model. Temporal patterns in nestling mortality indicate that brood reduction is prevalent at LES, offering support of the model's prediction that brood reduction should be occurring. Furthermore, the prediction that fratricide should have been the mechanism by which brood reduction was accomplished corresponded with observations of sibling aggression and parent behaviors. Other populations closer to their food supplies may exhibit less survival differential between broods of two and three and thus may not exhibit brood reduction behavior. That the survival differential at LES barely exceeded the brood reduction threshold is in accord with the fact that brood reduction is seen in some Osprey populations (Poole 1979, 1982; Jamieson et al. 1983) but not others (Green 1976, Stinson 1977, Poole 1982).

### MANAGEMENT IMPLICATIONS

The temporal patterns of nestling mortality at LES also have important management implications for Ospreys. Pre-fledged birds are frequently removed from populations for use in hacking practices in areas devoid of Ospreys. Ospreys have a propensity to return to their natal area as breeding adults, and the effect of nestling removals on the donor populations has received little attention. These data indi-

cate that once an LES nestling reaches four or five weeks of age, it is almost insured of reaching fledging age. Removing individuals of this age, or older, would have a near maximum effect on the population. The impact could only be reduced by removing individuals less than two or three weeks of age. Only then would compensatory mortality be operating. If a different population experienced less food stress than LES, and brood reduction occurred later in the nestling period, then older-aged nestlings could be removed with compensatory effects. Wise management decisions depend on an understanding of temporal patterns in nestling mortality of specific donor populations.

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