

TESTS OF THREE HYPOTHESES OF HATCHING ASYNCHRONY IN THE COMMON TERN

PATRICIA BLAIR BOLLINGER,^{1,3} ERIC K. BOLLINGER,^{1,3} AND
RICHARD A. MALECKI²

¹Department of Natural Resources, Cornell University, Ithaca, New York 14853 USA, and

²New York Cooperative Fish and Wildlife Research Unit, Department of Natural Resources,
Cornell University, Ithaca, New York 14853 USA

ABSTRACT.—We examined three hypotheses concerning hatching asynchrony in the Common Tern (*Sterna hirundo*). Survival of third-hatching "C-chicks" was significantly lower than that of "A-" and "B-chicks" in broods of three. In 2 yr when conditions did not appear favorable, survival was significantly higher in manipulated broods in which chicks hatched synchronously (73%) than in nonmanipulated broods (56%). Chicks in synchronous broods grew significantly faster than C-chicks and at a rate similar to A- and B-chicks. These results were inconsistent with the brood-reduction hypothesis, which predicts that hatching asynchrony will maximize brood success under conditions of food limitation. Chicks hatching from C-eggs grew significantly faster and survived at nonsignificantly higher rates when an older sibling was removed experimentally. These results were consistent with the hypothesis that C-chicks serve as insurance against loss of an older sibling. All three siblings, however, survived in 26% of nonmanipulated broods, which indicates that the sole function of the C-chick was not insurance. Predation on tern eggs was common and was correlated with numbers of migrating Ruddy Turnstones (*Arenaria interpres*). The percentage of time adults incubated was lower when only one egg had been laid than when two or three eggs were laid, and egg predation was most frequent during this initial stage. Although hatching asynchrony did not maximize chick survival, incubation before laying is completed may maximize overall nest success by protecting eggs from predators. Received 19 July 1989, accepted 28 April 1990.

MANY birds begin incubation before completion of a clutch of eggs. Hatching asynchrony is the result. Survival frequently decreases with hatching order (for reviews, see O'Connor 1978, Clark and Wilson 1981, Hahn 1981). One of the most widely cited explanations of hatching asynchrony is Lack's (1954) "brood reduction" hypothesis (i.e. hatching asynchrony is an adaptation for adjusting brood size to an unpredictable food supply). Asynchrony creates a size hierarchy among siblings. Subsequent sibling competition or more parental attention to larger siblings leads to starvation of the youngest chick when conditions are poor. Resources are not wasted on the chick least likely to survive, and starvation of the entire brood is prevented. Alternatively, the last egg may serve as "insurance" against loss of an earlier-laid egg or an older sibling in species in which the entire brood rarely fledges or survives to breed (Graves et

al. 1984). Hatching asynchrony ensures that the last sibling, in which the least resources have been invested, will be the one to die if the older siblings survive. A decrease in egg size with laying order can accentuate the size hierarchy within the brood through which the brood-reduction and insurance strategies operate (Slagsvold et al. 1984).

In Common Terns (*Sterna hirundo*; Nisbet 1973) and in larids in general (e.g. Parsons 1976), hatching is asynchronous, the last egg tends to be relatively small, and survival of the youngest sibling is reduced. Differential mortality by hatching order is usually viewed as adaptive in larids (but see Parsons 1976), either in terms of brood reduction (Langham 1972, Hahn 1981), insurance (Graves et al. 1984, Quinn and Morris 1986), or a strategy that combines both functions (Nisbet and Cohen 1975, Braun and Hunt 1983, Hebert and Barclay 1986). Few studies of larids, however, have offered strong experimental support for either hypothesis (but see Hahn 1981, Graves et al. 1984).

³ Present address: Department of Zoology, Eastern Illinois University, Charleston, Illinois 61920.

In contrast, several recent hypotheses view differential mortality within broods simply as a side effect of hatching asynchrony or of incubation before the clutch is completed (reviewed by Hussell 1972, Clark and Wilson 1981). In fact, in apparent contrast to the predictions of the brood-reduction hypothesis, the majority of experimental studies that compare normal, asynchronously hatching broods with manipulated, synchronously hatching broods have failed to detect higher survival rates in asynchronous broods (see reviews in Amundsen and Stokland 1988, Skagen 1988). Specifically, relatively high survival was recorded in synchronous broods of gulls (Hebert and Barclay 1986; but see Hahn 1981), cormorants (Shaw 1985, Amundsen and Stokland 1988), herons (Fujioka 1985, but see Mock and Ploger 1987), and passerines (Slagsvold 1982; Haydock and Ligon 1986; Gibbons 1987; Skagen 1987, 1988; but see Magrath 1989). In most of these studies chick growth was also similar in synchronous and asynchronous broods (see Werschkul 1979). Although only a few of these studies indicated that conditions were food-limited (Hebert and Barclay 1986, Skagen 1988, Magrath 1989), they call into question the general applicability of Lack's hypothesis. Stokland and Amundsen (1988) suggested that selection pressures to begin incubation before clutch completion deserve critical attention.

We tested the brood-reduction and insurance hypotheses in the Common Tern under conditions of food limitation. We also attempted to determine whether onset of incubation before clutch completion could reflect predation pressure during the egg-laying period (the "egg protection hypothesis"; Parsons 1976). In this species, partial incubation begins with the first of 3 eggs (Nisbet and Cohen 1975), and the chicks hatch asynchronously, usually over 1.5-3 days (Courtney 1979). Mortality is higher for last-hatching "C-chicks" than for "A-" or "B-chicks" (Langham 1972, Nisbet 1973). Our objectives were to determine (1) whether manipulated broods with synchronous hatching were as successful as nonmanipulated broods; (2) the frequency with which all 3 chicks in a brood survived; (3) whether chicks hatching from C-eggs had higher survival rates after removal of an older sibling; and (4) whether constancy of incubation was related to frequency of egg predation.

METHODS

We studied Common Terns breeding on Oneida Lake, Oswego County, New York, in 1983-1985. Approximately 350 pairs of terns nested on two small, rocky shoals (0.046 and 0.120 ha). We marked each egg with waterproof ink and weighed eggs in 1983-1984 with a 50-g Pesola scale. We weighed most eggs within 24 h of laying; other eggs were weighed twice at a 7-10-day interval, and the initial weight was determined as in Rahn et al. (1976). We checked each nest daily for evidence of egg predation. To aid in the recapture of chicks, in 1983-1984 we enclosed groups of nests with 0.4-m-high wire mesh fences before hatching (Nisbet and Drury 1972a). During the hatching period we checked each nest 1-2 times daily for new chicks. Each chick was weighed at hatching and banded with a USFWS aluminum leg band.

We recorded chick growth and survival in 1983-1984. In 1985 we recorded survival only. We searched for dead chicks daily in 1983-1984. In 1983 each chick was weighed daily until it died or escaped from its enclosure. In 1984 we weighed each chick within its enclosure every 1-2 days until days 11-14, and subsequently we made four colony-wide chick censuses. These censuses, which were facilitated by the small size and sparse vegetation of the islands, were virtually complete (>95%) counts of chicks (Bollinger 1988). Chicks alive at \geq day 18 in 1983-1984 were considered to have survived, because some chicks were able to escape from the enclosures before fledging at \geq 22 days of age (Nisbet and Drury 1972a). In 1985 we searched the area around each nest daily until the chicks reached day 10, and subsequently we made three colony-wide censuses. We considered chicks alive at \geq day 10 in 1985 to have survived, because 92% of 73 chick deaths occurred by this age in 1983-1984 (see also Langham 1972, Nisbet and Drury 1972a).

Brood types studied.—We studied nonmanipulated, asynchronously hatching ("asynchronous") broods of 3 chicks, raised by their own parents, in 1983-1985 ($n = 16$ broods in 1983, 35 in 1984, and 15 in 1985). In 1984 we also created 18 "A/B-removal" broods from nests originally containing 3 eggs. We removed the first or second egg (4 nests) or chick (at \leq 2 days of age; 14 nests) before hatching of the C-egg. The chick from the C-egg in an A/B-removal brood was denoted the "B-chick" and its older sibling, the "A-chick."

In 1984 we created 20 "synchronous" broods by placing together 3 randomly selected chicks hatching within 12 (\geq 70% of the broods) to 20 h of one another. Chicks in synchronous broods (i.e. "synchronous chicks") were transferred when first found, within 12 (\geq 68% of the broods) to 24 h of hatching. (No deaths had occurred among asynchronous chicks when first found on the day of hatching.) In 1985 we created 15 synchronous broods of 3 chicks, in which siblings

hatched within 24 h of one another and were transferred within 14 ($\geq 60\%$ of the broods) to 24 h of hatching. In each year only adults that laid 3 eggs were given synchronous broods.

Incubation constancy and egg predation.—In 1985 we used a blind to observe 58 nests, each for an average of 5 consecutive days. Three 1-h observations were made daily from 28 May to 9 June, with morning (0845–1300) and afternoon (1300–1800) sessions on alternate days. The presence or absence of incubating terns at each nest was recorded at 5-min intervals. At the beginning and end of each session we recorded the number of eggs depredated at each focal nest and the number of Ruddy Turnstones (*Arenaria interpres*) visible on the island.

Statistical methods.—We calculated individual chick growth rates from weights at days 1–11, a period in which growth was exponential (LeCroy and LeCroy 1974). Linear regressions of $\ln(\text{weight})$ vs. age were performed for all chicks for which at least 4 weights were available. We used *t*-tests to compare mean growth rates of groups of chicks, and Chi-square and Fisher's exact tests to compare numbers of chicks that survived in different groups. We combined data from 1984 and 1985 for analysis when significant differences ($P < 0.05$) in survival rates (Chi-square tests) or in means (*t*-tests) and variances (*F*-tests, Snedecor and Cochran 1980: 98) did not occur between years.

RESULTS

Egg weights and hatching asynchrony.—Clutches of 3 eggs represented 70% of all clutches. Egg weight decreased as each egg was laid in 3-egg clutches (two-way ANOVA, $P < 0.0001$, $n = 235$ clutches; paired *t*-tests, $P < 0.05$). Although chicks used in synchronous broods were selected randomly, eggs from which synchronous chicks hatched ($\bar{x} \pm \text{SD} = 20.7 \pm 1.3$ g, $n = 50$) were similar in weight to eggs of C-chicks (20.8 ± 1.7 g, $n = 31$; *t*-test, $P > 0.75$) and lighter than eggs of A-chicks (21.4 ± 1.7 g, $n = 25$; $P < 0.05$) in asynchronous broods.

Laying intervals averaged 1.9 ± 0.8 days between the A- and B-eggs, and 1.8 ± 0.6 days between the B- and C-eggs ($n = 118$ clutches). Asynchronous broods hatched over 1–3 days, with mean intervals of 0.7 ± 0.6 days between the A- and B-chicks, and 1.2 ± 0.7 days between the B- and C-chicks ($n = 50$ broods). No asynchronous brood hatched in ≤ 24 h; in contrast, all synchronous broods hatched within 24 h, with a mean interval of 0.5 ± 0.5 days ($n = 35$).

Seasonal variation.—Clutch initiation occurred from 24 May to 24 July in 1983, 19 May to 25 July in 1984, and 15 May to 23 July in 1985.

Approximately 75% of all clutches were initiated in the first one third of the laying period in 1983 and 1984 (i.e. by 10 June), and in the first one half of the season in 1985 (by 15 June). Our analyses included only chicks that hatched from clutches started during or near these major periods of clutch initiation. We studied asynchronous and synchronous chicks that hatched between 21 June and 5 July in 1983, 15 June and 16 July in 1984, and 17 June and 11 July in 1985; chicks continued to hatch at least until 6 August 1983, 11 August 1984, and 1 August 1985.

In no year were there significant correlations between hatching date and chick survival (1983: Spearman's $\rho = -0.183$, $P > 0.10$, $n = 60$; 1984: $\rho = -0.047$, $P > 0.25$, $n = 305$; 1985: $\rho = -0.120$, $P > 0.25$, $n = 90$) or chick growth (1983: $\rho = 0.40$ – 0.67 , $P > 0.10$; 1984: $\rho = -0.12$ – 0.08 , $P > 0.50$). Furthermore, in 1984, the year in which we studied chicks over the longest hatching period, survival of asynchronous chicks was almost identical in the middle of the focal hatching period (27 June–10 July; 56% survival, $n = 45$) and the remainder of this period (57% survival, $n = 58$; $P = 0.90$). Therefore, within each year we combined all chicks for further analyses.

The brood-reduction hypothesis.—In order to evaluate the extent of food limitation in the experimental years, we compared survival rates in 1984 and 1985 with those in 1983. The overall survival rate (i.e. all siblings combined) in asynchronous broods was significantly higher in 1983 than in 1984 or 1985, although 1984 and 1985 did not differ for either asynchronous or synchronous broods (Table 1). Similarly, survival was higher in 1983 than in 1984 and 1985 combined for both A- and B-chicks in asynchronous broods ($P < 0.025$), although survival of C-chicks did not vary significantly between these years ($P > 0.50$; Fig. 1). The average growth rates of A- and C-chicks that survived were greater in 1983 than in 1984 ($P < 0.05$; Table 2). C-chicks that survived grew significantly faster than those that died; similar trends were observed for B-chicks and synchronous chicks (Table 2). These results indicate that food was not plentiful in the experimental years.

Chick survival varied with hatching order in asynchronous broods. A- and B-chicks survived more often than C-chicks (Fig. 1) and at rates similar to one another each year ($P > 0.10$). Growth rates also varied in 1984 (ANOVA, $P < 0.005$): A- and B-chicks that survived had similar

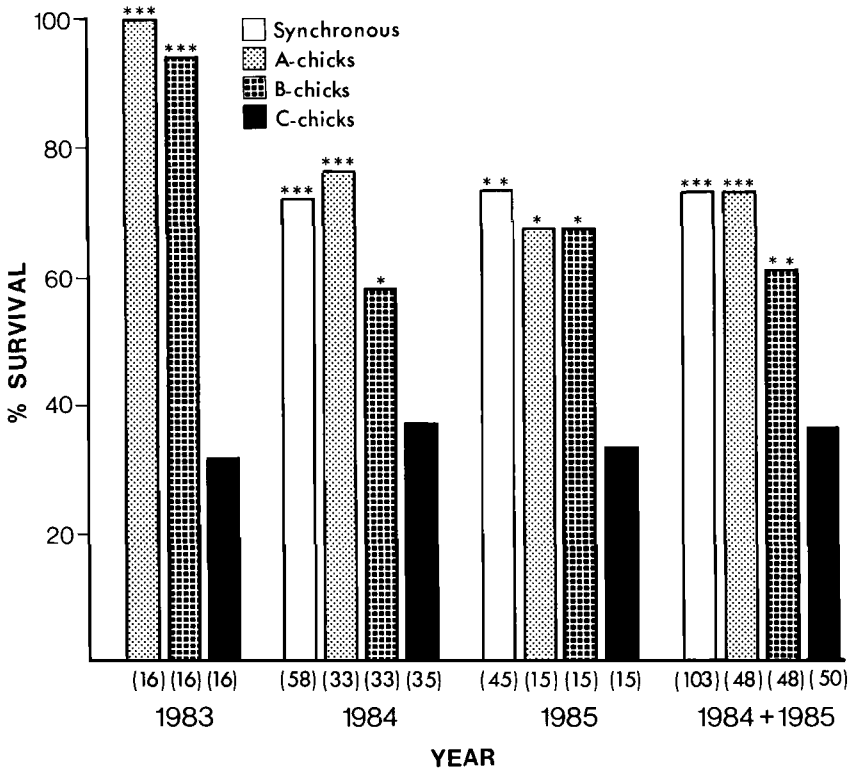


Fig. 1. Variation in rates of survival among synchronous chicks and A-, B-, and C-chicks in asynchronous 3-chick broods of Common Terns. Asterisks indicate differences in survival rates between C-chicks and the other chick classes (Chi-square tests, 1 df). Sample sizes are in parentheses; * = $P < 0.10$; ** = $P < 0.025$; *** = $P < 0.005$.

growth rates, but both grew faster than C-chicks (Table 2). In contrast, in 1983 there were no significant differences in growth rate among A-, B-, or C-chicks that survived (ANOVA, $P > 0.50$; Table 2).

Asynchrony did not maximize brood success. The mean number of chicks that survived per brood and the overall survival rate were higher in synchronous than in asynchronous broods in both 1984 and 1985 (Table 1). Synchronous chicks survived more often than C-chicks (Fig. 1) and at rates similar to those of A-chicks ($P > 0.50$) and B-chicks ($P > 0.10$) in both years. Furthermore, synchronous chicks that survived grew faster than C-chicks ($P < 0.01$) and similarly to A-chicks ($P > 0.25$) and B-chicks ($P > 0.90$; Table 2), with mean weights at days 13-14 similar in both brood types (synchronous: 88.1 ± 17.6 g, $n = 12$; asynchronous: 85.2 ± 9.7 g, $n = 19$; t -test, $P > 0.50$). Age at death also did not differ significantly between synchro-

nous ($\bar{x} = 6.7 \pm 4.2$ days, $n = 28$) and asynchronous chicks (5.8 ± 2.9 days, $n = 64$) in 1984 (t -test, $P > 0.90$) or 1985 ($P > 0.10$). Similarly, the proportion of broods in which all 3 chicks died, and the ratio of partial brood success (1-2 chicks surviving) to complete brood failure, did not differ significantly between brood types (Table 3). However, the proportion of broods in which all 3 chicks survived tended to be higher for synchronous than asynchronous broods (Table 3).

The insurance hypothesis.—Chicks hatching from C-eggs grew significantly faster in A/B-removal broods (B-chicks) than in asynchronous 3-chick broods (C-chicks), and survived at nonsignificantly higher rates (Table 4). B-chicks in A/B-removal broods grew and survived at rates almost identical to those of B-chicks in asynchronous 3-chick broods (Table 4). All 3 siblings survived in 31% (1983, $n = 16$), 20% (1984, $n = 35$), and 33% (1985, $n = 15$) of asyn-

TABLE 1. Comparison of Common Tern brood success between asynchronous and synchronous 3-chick broods and between years.^a Within each brood type, values followed by the same letter do not differ between years ($P > 0.05$). Values for 1984 + 1985 were compared only with values for 1983. Sample sizes are in parentheses.^b

Year	Asynchronous	Synchronous	Asynch. vs. Synth.
No. surviving per brood (\pmSD)			
1983	2.3 \pm 0.6a (16)	—	—
1984	1.7 \pm 1.0b (33)	2.2 \pm 0.9a (18)	0.05 < P < 0.10
1985	1.7 \pm 1.2ab (15)	2.2 \pm 0.9a (15)	P > 0.25
1984 + 1985	1.7 \pm 1.0b (48)	2.2 \pm 0.9 (33)	P < 0.05
Percent overall survival			
1983	75.0a (48)	—	—
1984	56.3b (103)	72.4a (58)	P < 0.05
1985	55.6b (45)	73.3a (45)	0.05 < P < 0.10
1984 + 1985	56.1b (148)	72.8 (103)	P < 0.01

^a Chi-square tests with 1 df were used for number surviving (% overall survival); Mann-Whitney U -tests were used for no. surviving per brood.

^b Sample sizes for number surviving per brood were less than one third times those for % overall survival when fates of some of the siblings were unknown.

chronous broods, and in 42% (1984, $n = 19$) and 47% (1985, $n = 15$) of synchronous broods.

Egg predation and incubation constancy.—Predation of at least one egg occurred in 31% of 303 nests from 27 May to 9 June 1983, 51% of 329 from 24 May to 5 June 1984, and 45% of 247 from 28 May to 9 June 1985; by these dates 68%, 59%, and 45%, respectively, of all clutches had been started. Rates of predation were lower after these dates. In 1985 daily numbers of migrating Ruddy Turnstones and egg predation events were positively correlated between 28

May and 9 June ($r = 0.73$, $P < 0.01$, $n = 11$ days). In 9 of 19 instances of predation among focal nests, the eggs either had a small puncture or were split into two pieces; in the remaining instances the eggs were missing. We observed turnstones eating the contents of previously cracked eggs, and we observed a turnstone peck 1 of 2 eggs in a temporarily unattended nest. Ruddy Turnstones were generally ignored by terns. Of 19 focal nests that suffered predation, 16 were attended—at least sporadically—by an adult during the last observation period before egg loss.

Our activity in the colony did not appear to influence egg predation. Of the 19 predation events in focal nests, 13 (68%) occurred while we were off the island or in the blind. Predation patterns among the focal nests were similar to those observed in the entire colony (Table 5), although we created greater disturbance among focal nests. Furthermore, Ruddy Turnstones took flight more readily and returned to the colony more slowly than did the terns after human disturbance.

Incubation constancy varied among egg-laying stages (i.e. 1, 2, or 3 eggs laid) of 3-egg clutches observed at all 3 stages (Friedman's test [Conover 1980: 299], $P < 0.005$, $n = 5$). For clutches observed during more than 1 stage, incubation constancy was significantly lower at the 1-egg stage than at either the 2- or 3-egg stage, but it was similar at the 2- and 3-egg stages (Table 6). Similarly, egg loss occurred more frequently at the 1-egg stage than at either the 2- or 3-egg stage, but the 2- and 3-egg stages

TABLE 2. Mean growth rates^a (\pm SD) of Common Tern chicks that survived and chicks that died (1983 and 1984), by hatching order (A = first; B = second; C = third). Within years, values followed by the same letter do not differ significantly (t -tests, $P > 0.05$). Sample sizes are in parentheses.

Chick class	Chicks that survived	Chicks that died ^b
Asynchronous 1983		
A	0.179 \pm 0.017a (16)	— ^c
B	0.170 \pm 0.016a (16)	—
C	0.173 \pm 0.025a (7)	-0.027 \pm 0.061 (5)**
Asynchronous 1984		
A	0.167 \pm 0.014a (21)	0.166 \pm 0.033 (6) ^{NS}
B	0.163 \pm 0.019a (15)	0.124 \pm 0.078 (13)*
C	0.145 \pm 0.016b (12)	0.000 \pm 0.085 (17)**
Synchronous 1984		
—	0.163 \pm 0.019 (42)	0.110 \pm 0.085 (11)*

^a Growth rates are $\ln(g)/$ day weight gains in the first 11 days.

^b t -tests between chicks that survived and chicks that died: ** = $P < 0.005$; * = $0.05 < P < 0.10$; ^{NS} = $P > 0.50$.

^c Samples were too small to include in the analysis.

TABLE 3. Rates of partial brood success (PBS; 1-2 chicks survive per brood), complete brood failure (CBF), and whole brood survival (WBS) in asynchronous and synchronous 3-chick broods of the Common Tern (1984 and 1985 combined). Sample sizes are in parentheses.

	Brood type		Asynch. vs. Synch.	Prediction
	Asynch.	Synch.		
No. PBS/No. CBF	3.8 (30/8)	8.5 (17/2)	$P > 0.25^a$	Asynch. > Synch. ^c
% CBF	16.0 (50)	5.7 (35)	$P > 0.10^b$	Asynch. < Synch. ^c
% WBS	24.0 (50)	44.1 (34)	$0.05 < P < 0.10^b$	Asynch. > Synch. ^d

^a Fisher's exact test.

^b Chi-square test, 1 df.

^c Prediction based on brood-reduction hypothesis; from Hahn (1981).

^d Prediction based on sibling rivalry reduction hypothesis; from Hahn (1981).

did not differ significantly (Table 5). Incubation constancy at the 1-egg stage was similar for nests that were damaged during this stage ($65.6\% \pm 45.6$, $n = 10$) and those that were not ($68.2\% \pm 35.7$, $n = 25$) (Mann-Whitney *U*-test, $P > 0.95$). However, incubation constancy at the 2- and 3-egg stages tended to be lower for nests that were depredated during these stages ($63.4\% \pm 25.0$, $n = 4$) than for those that were not ($92.3\% \pm 13.8$, $n = 21$; $P = 0.07$).

DISCUSSION

The brood-reduction hypothesis.—According to the brood-reduction hypothesis, the competitive weakness of younger siblings facilitates their early death when feeding conditions are poor (Lack 1954). This increases the chances of

survival of the older siblings and maximizes the number of young that fledge. Furthermore, brood reduction should minimize the rate of complete brood failure and maximize the ratio of partial brood success to complete failure (Hahn 1981).

Conditions were sufficient for a brood-reduction strategy to operate at our colonies. C-eggs in 3-egg clutches hatched later and were significantly lighter than A- or B-eggs. Chick mortality was common and occurred early in the nestling period. C-chicks survived less often than A- or B-chicks in all three years. C-chicks also grew significantly more slowly than A- or B-chicks in 1 of 2 years. The major cause of chick mortality appeared to be starvation. Growth rates tended to be lower for chicks that died than for survivors. These dif-

TABLE 4. Comparison of survival and growth rates^a between B-chicks in A/B-removal broods (which hatched from C-eggs) and chicks in asynchronous 3-chick broods of Common Terns in 1984.^b Values followed by the same letter do not differ significantly between chick classes ($P > 0.05$).^c Sample sizes are in parentheses.

Brood type/ chick class	Survival (%)	Growth rate of survivors ($\bar{x} \pm SD$)
A/B-removal		
B	55.6ab (18)	$0.162 \pm 0.018a$ (9)
Asynch. 3-chick		
A	75.8a (33)	$0.167 \pm 0.014a$ (21)
B	57.6ab (33)	$0.163 \pm 0.019a$ (15)
C	37.1b (35)	$0.145 \pm 0.016b$ (12)

^a Growth rates are $\ln(g)/\text{day}$ weight gains in the first 11 days.

^b Chi-square tests with 1 df were used for number surviving; *t*-tests were used for growth rate.

^c For % survival of B- vs. C-chicks in 3-chick broods, $0.05 < P < 0.10$.

TABLE 5. Variation in frequency of egg predation by stage of egg laying (number of eggs laid) in the Common Tern, 28 May-9 June, 1985. Values followed by the same letter do not differ significantly between egg-laying stages (Chi-square tests with 1 df, $P > 0.05$).^a Nests in the entire colony were checked daily; focal nests (observed during the incubation study) were checked 6 times daily.

	Entire colony	Focal nests
Predation events/nest-day ^b		
1-egg stage	0.15a	0.14a
2-egg stage	0.06b	0.05ab
3-egg stage	0.04b	0.04b
<i>p</i> ^c	<0.005	<0.05
Total predation events (<i>n</i>)		
	112	19
Total nests (<i>n</i>)		
	249	58
Total nest-days (<i>n</i>)		
	1,826	268

^a For focal nests at the 1-egg vs. 2-egg stages, $0.05 < P < 0.10$.

^b Nest-days were calculated by summing the number of days each nest was present.

^c Chi-square test, 1-egg vs. 2-egg vs. 3-egg stage.

TABLE 6. Variation in incubation constancy by stage of egg laying (number of eggs laid), for Common Tern clutches observed during 2 stages, 28 May–9 June, 1985. Sample sizes are in parentheses.

Stage of egg laying	% time spent incubating ($\bar{x} \pm SD$)	P^a
1-egg	68.3 \pm 34.9 (20)	$P < 0.001$
2-egg	94.5 \pm 10.7 (20)	
1-egg	53.1 \pm 38.2 (6)	$P < 0.05$
3-egg	94.9 \pm 8.1 (6)	
2-egg	81.6 \pm 23.6 (11)	0.05 $< P < 0.10$
3-egg	90.8 \pm 12.9 (11)	

^a Wilcoxon signed-rank test.

ferences were minimum estimates, as growth was not measured for chicks that died within 4 days of hatching (33% of 105 dead chicks). These chicks showed little or no weight gain. Although bodies of young chicks deteriorated rapidly and were difficult to find among the rocks and vegetation, we found the bodies of 69% of the chicks that died. There was no evidence of predation on chicks, nor was there unusually poor weather in any year.

The brood-reduction hypothesis states that asynchronous broods should be more successful than synchronous broods if feeding conditions are poor. Even if brood reduction is a strategy that augments brood success during poor years and reduces success during good years, it can be adaptive only if gains made in poor years outweigh losses suffered in good years. Conditions did not appear favorable for chicks in 1984 and 1985, when nearly half of all chicks in normal 3-chick broods apparently died of starvation. Rates of chick survival (56% in normal broods) and growth were significantly lower in these years than in 1983. Although chick survival rates vary widely among studies of Common Terns (Morris et al. 1976), starvation rates are difficult to determine given unknown levels of predation. Other studies in which predation on chicks was apparently not a factor reported fledging rates similar to or higher than ours; e.g. 51, 60, and 89% for 3-chick broods (Langham 1972) and, for all brood sizes combined, 68–79% (LeCroy and LeCroy 1974) and 52–67% (Safina et al. 1988). Adult terns frequently stole fish from chicks in 1984, a behavior that may occur during food shortages (Hays 1970, Monaghan et al. 1989). This was not observed in 1983.

Contrary to the predictions of the brood-reduction hypothesis, survival was significantly higher in synchronous than asynchronous broods. Synchronous chicks also grew significantly faster than C-chicks and similarly to A- and B-chicks. Asynchrony did not reduce the rate of complete brood failure or increase the ratio of partial brood success to complete failure, as predicted. In fact, the differences were in the opposite direction (see also Gibbons 1987, Magrath 1989). The average age at death was similar in both brood types, which indicates that parents of synchronous chicks did not invest unduly in chicks that died (see also Shaw 1985, Skagen 1988; but see Haydock and Ligon 1986, Gibbons 1987). Furthermore, survival of A- and B-chicks varied between years, but that of C-chicks did not (see also Shaw 1985; but see Langham 1972). Thus, it appeared that C-chick survival depended less on food supply than did survival of older siblings (in contrast to one of the major predictions of the brood-reduction hypothesis).

The brood-reduction hypothesis implies that C-chicks are hatched asynchronously so as not to reduce survival of older siblings. However, A- and B-chicks in asynchronous broods did not survive more often than synchronous chicks, which indicates that asynchrony did not reduce costly competition on older siblings. Moreover, survival of B-chicks was significantly lower in 3-chick broods than in naturally occurring 2-chick broods (Bollinger 1988). We suggest that the presence of C-chicks did reduce survival of B-chicks (see also Graves et al. 1984, Hebert and Barclay 1986).

C-chicks in asynchronous broods may have starved unnecessarily (Bryant 1978, Werschkul 1979, Skagen 1988). Adults may have fed siblings more equitably in synchronous broods, as differences in growth rate among siblings tended to be smaller in these broods (Bollinger 1988). The size of a chick relative to its siblings appeared more important than absolute size in influencing its survival, because egg weights were similar for C-chicks and synchronous chicks.

Our results are consistent with several recent experimental studies that have failed to detect higher survival rates in normal, asynchronous broods than in synchronous broods. Among larvae, synchronous Herring Gull (*Larus argentatus*) chicks survived as often as asynchronous chicks in a year when conditions appeared poor; syn-

chronous chicks grew similarly to A-chicks and faster than B- and C-chicks (Hebert and Barclay 1986). In contrast, manipulated, synchronous broods of Laughing Gulls (*L. atricilla*) had lower fledging rates, more complete failures, fewer complete successes, and a lower ratio of partial success to complete failure than asynchronous broods (Hahn 1981). It is not clear why Hahn's results differed from ours.

Higher fledging rate is not necessarily equivalent to greater lifetime reproductive success, if increased reproductive effort by parents will lower their future reproductive output. We do not have data to address this point. In addition, survival after fledging may be lower for larid chicks in larger broods (Nisbet and Drury 1972b), although Parsons et al. (1975) recorded lower postfledging survival in larger broods of Herring Gulls in only 1 of 3 years. Within the normal range of brood sizes, Glaucous-winged Gull (*L. glaucescens*) chicks that fledged in larger broods survived at least as well after fledging as those in smaller broods (Ward 1973). In our study, 7 of 75 synchronous chicks (9.3%) and 4 of 83 asynchronous chicks (4.8%) that fledged in 1984-1985 were captured as breeding adults in 1988 (H.-W. Yuan unpubl. data). Chicks that fledged in synchronous broods apparently did not return at lower rates. Furthermore, growth rates between days 1-11 and weights at days 13-14 were similar in both brood types, which suggests that synchronous fledglings were similar in quality to asynchronous young.

The insurance hypothesis.—According to the insurance hypothesis, the full brood rarely fledges (or survives to breed), and the last egg is laid as insurance in case an older chick dies or fails to hatch (Graves et al. 1984). The brood-reduction and insurance hypotheses are not mutually exclusive; asynchronous hatching may provide insurance benefits under poorer conditions and allow the entire brood to be raised under more favorable conditions (Nisbet and Cohen 1975). However, if the sole function of the C-egg is insurance, the C-chick should rarely fledge unless the A- or B-egg or chick dies. Although this has been suggested to be the usual case for Common Terns (e.g. Nisbet and Cohen 1975, Nisbet 1978), we found that survival of all 3 chicks was not rare in asynchronous broods (26%; see also Langham 1972, Nisbet et al. 1984) or synchronous broods (44%). The insurance hypothesis also predicts that survival of chicks from C-eggs will increase if an older sibling dies. Our data

were consistent with this prediction. When first or second eggs or chicks were removed (A/B-removal broods), chicks hatched from C-eggs (B-chicks) grew significantly faster than C-chicks in 3-chick broods and survived more often than C-chicks, although the latter difference was not significant (see also Quinn and Morris 1986).

In sum, our data did not strongly support the insurance hypothesis. Given the results of the hatching synchrony experiment, mortality of the C-chick caused by asynchronous hatching does not appear to be beneficial in this species. Although egg size might be expected to increase, rather than decrease, with laying order to offset the negative effects of asynchrony (Slagsvold et al. 1984), we found no effect of egg size on survival in nonmanipulated 3-chick broods (Bollinger in prep.; but see Nisbet 1973, 1978). Decreased egg size may simply reflect the condition of the female as egg laying progresses and incubation begins (Houston et al. 1983, Pierotti and Bellrose 1986). A Common Tern's clutch accounts for approximately 45% of the female's body weight (Wiggins and Morris 1987), and size of the C-egg can be related to food intake by females (Nisbet 1973).

Alternative explanations of hatching asynchrony.—Hussell (1972) and Clark and Wilson (1981) proposed that some birds begin incubation before clutch completion for reasons other than to ensure sibling competition and differential mortality within the brood. Early incubation may speed hatching or fledging, so the young can make full use of declining resources, or so the time during which the nest is vulnerable to predation is reduced (Hussell 1972). However, the incubation and nestling periods of Common Terns are long (6-7 weeks total) relative to the hatching interval (1-3 days), so benefits from earlier hatching or fledging are probably minimal (Shaw 1985). Incubation may help to maintain egg viability (Arnold et al. 1987), but this seems unlikely to be important for the typically small tern clutch. Hatching asynchrony may spread out peak food demands of young (Bryant 1978). This assumption predicts that asynchrony will maximize brood success (this was not observed), or will reduce parental stress. An alternative function of the sibling dominance hierarchy to that of facilitating brood reduction may be to reduce wasteful sibling rivalry, thus increasing the proportion of nests that fledge the whole brood (Hahn 1981). In our study, whole brood success tended

to be less common for asynchronous broods. Degree of hatching asynchrony may also reflect physiological constraints on adults, such as food availability during the egg-laying period (Pierotti and Bellrose 1986).

Clark and Wilson (1981) suggested that early incubation minimizes the vulnerability of the nest to whole nest predation by speeding fledging to an extent determined by the relative risk of predation during the preincubation and fledging stages (see also Briskie and Sealy 1989). Whole nest predation after hatching is not common in Common Terns. Somewhat analogously, other researchers have suggested that, to reduce egg predation, some birds begin incubation before completion of laying (Blaker 1969, Parsons 1976; see also Skipnes 1983). Open-nesting colonial birds such as larids may be particularly susceptible to a variety of egg predators. Although hatching success varies widely among studies of Common Terns (Morris et al. 1976), Ruddy Turnstones can be important predators of tern eggs (Brearey and Hilden 1985, Morris and Wiggins 1986), and egg predation by conspecifics is common among gulls (e.g. Parsons 1976). Incubation may prevent egg predation more effectively than egg guarding (Thompson and Raveling 1987). Common Terns resumed incubation after chasing Ruddy Turnstones from previously unattended nests (Morris and Wiggins 1986, this study). Ruddy Turnstones pecked Sooty Tern (*Sterna fuscata*) eggs when incubating terns momentarily left their nests (Crossin and Huber 1969), and Arctic Tern (*S. paradisaea*) eggs were usually lost only when adults had been scared off their nests by Common Gulls (*Larus canus*) (Skipnes 1983). Furthermore, incubation may reduce predation when terns do not recognize another species as a potential egg predator, as may be the case with Ruddy Turnstones (Parkes et al. 1971).

Alternatively, egg protection may be a side effect—rather than the primary selective agent—of early incubation. This would help explain the consistency in patterns of incubation onset among larids regardless of observed predation pressure. Early incubation itself may be useful for some other reason (see above), or it may be an incidental trait without adaptive significance that results from constraints on hormonal mechanisms that control egg laying and incubation (Mead and Morton 1985).

In our experience egg predation was common during the egg-laying period. Ruddy Turnstone

numbers and predation events were positively correlated, and egg losses fit descriptions of turnstone predation in other tern colonies (Parkes et al. 1971, Morris and Wiggins 1986). Although turnstones were present for only a relatively short time, this coincided with the initiation of a large portion (45–68%) of the Common Tern nests each year. Incubation constancy increased and egg predation decreased significantly during egg laying. Incubation also increased through egg laying in other studies of Common Terns (Nisbet and Cohen 1975, Courtney 1979), and Morris and Wiggins (1986) found that Ruddy Turnstone predation on Common Tern eggs occurred most often in nests containing only 1 egg. Predation of A-eggs exceeded that of B- and C-eggs in Herring (Parsons 1976) and Glaucous-winged gulls (Verbeek 1988). These results support the hypothesis that consistent incubation in larids helps to protect eggs from predators, regardless of the reasons for beginning incubation.

We propose that chick mortality due to hatching asynchrony may not be adaptive in Common Terns. If early incubation is a result of selective pressures related to egg predation, it may maximize overall nest success even if it reduces chick survival. Intermittent incubation during early egg laying may reflect a balance between positive effects of early incubation and negative effects of hatching asynchrony. Alternatively, if early incubation is an incidental trait, egg protection may mitigate some of the costs incurred by this behavior.

ACKNOWLEDGMENTS

We thank J. L. Forney, director of the Cornell Biological Field Station, for financial and logistical assistance throughout this study. The New York State Department of Environmental Conservation also provided logistical support. We thank A. Ducey, E. Jones, and L. Sloate for assistance in the field, and T. A. Gavin, G. L. Hunt Jr., R. D. Morris, and P. Stouffer for manuscript review. This study was conducted while P. B. Bollinger was supported by a N.S.F. Graduate Fellowship and Cornell University A. D. White Fellowship. This is contribution no. 117 of the Cornell Biological Field Station.

LITERATURE CITED

- AMUNDSEN, T., & J. N. STOKLAND. 1988. Adaptive significance of asynchronous hatching in the Shag: a test of the brood reduction hypothesis. *J. Anim. Ecol.* 57: 329–344.

- ARNOLD, T. W., F. C. ROHWER, & T. ARMSTRONG. 1987. Egg viability, nest predation, and the adaptive significance of clutch size in prairie ducks. *Am. Nat.* 130: 643-653.
- BLAKER, D. 1969. Behaviour of the Cattle Egret *Ardeola ibis*. *Ostrich* 40: 75-129.
- BOLLINGER, P. B. 1988. Hatching asynchrony and factors influencing chick survival in the Common Tern. M.S. thesis, Ithaca, Cornell Univ.
- BRAUN, B. M., & G. L. HUNT JR. 1983. Brood reduction in Black-legged Kittiwakes. *Auk* 100: 469-476.
- BREAREY, D., & O. HILDEN. 1985. Nesting and egg-predation by Turnstones *Arenaria interpres* in larid colonies. *Ornis Scandinavica* 16: 283-292.
- BRISKIE, J. V., & S. G. SEALY. 1989. Nest-failure and the evolution of hatching asynchrony in the Least Flycatcher. *J. Anim. Ecol.* 58: 653-665.
- BRYANT, D. M. 1978. Establishment of weight hierarchies in the broods of House Martins *Delichon urbica*. *Ibis* 120: 16-26.
- CLARK, A. B., & D. S. WILSON. 1981. Avian breeding adaptations: hatching asynchrony, brood reduction, and nest failure. *Q. Rev. Biol.* 56: 253-277.
- CONOVER, W. J. 1980. Practical nonparametric statistics, 2nd ed. New York, John Wiley and Sons.
- COURTNEY, P. 1979. Seasonal variation in intra-clutch hatching intervals among Common Terns *Sterna hirundo*. *Ibis* 121: 207-211.
- CROSSIN, R. S., & L. N. HUBER. 1969. Sooty Tern egg predation by Ruddy Turnstones. *Condor* 71: 371-373.
- FUJIOKA, M. 1985. Food delivery and sibling competition in experimentally even-aged broods of the Cattle Egret. *Behav. Ecol. Sociobiol.* 17: 67-74.
- GIBBONS, D. W. 1987. Hatching asynchrony reduces parental investment in the Jackdaw. *J. Anim. Ecol.* 56: 403-414.
- GRAVES, J., A. WHITEN, & P. HENZI. 1984. Why does the Herring Gull lay three eggs? *Anim. Behav.* 32: 798-805.
- HAHN, D. C. 1981. Asynchronous hatching in the Laughing Gull: cutting losses and reducing rivalry. *Anim. Behav.* 29: 421-427.
- HAYDOCK, J., & J. D. LIGON. 1986. Brood reduction in the Chihuahuan Raven: an experimental study. *Ecology* 67: 1194-1205.
- HAYS, H. 1970. Common Terns pirating fish on Great Gull Island. *Wilson Bull.* 82: 99-100.
- HEBERT, P. N., & R. M. R. BARCLAY. 1986. Asynchronous and synchronous hatching: effect on early growth and survivorship of Herring Gull, *Larus argentatus*, chicks. *Can. J. Zool.* 64: 2357-2362.
- HOUSTON, D. C., P. J. JONES, & R. M. SIBLY. 1983. The effect of female body condition on egg laying in Lesser Black-backed Gulls *Larus fuscus*. *J. Zool.* London 200: 509-520.
- HUSSELL, D. J. T. 1972. Factors affecting clutch size in arctic passerines. *Ecol. Monogr.* 42: 317-364.
- LACK, D. 1954. The natural regulation of animal numbers. London, Oxford Univ. Press.
- LANGHAM, N. P. E. 1972. Chick survival in terns (*Sterna* spp.) with particular reference to the Common Tern. *J. Anim. Ecol.* 41: 385-395.
- LECROY, M., & S. LECROY. 1974. Growth and fledging in the Common Tern (*Sterna hirundo*). *Bird-Banding* 45: 326-340.
- MAGRATH, R. D. 1989. Hatching asynchrony and reproductive success in the Blackbird. *Nature* 339: 536-538.
- MEAD, P. S., & M. L. MORTON. 1985. Hatching asynchrony in the Mountain White-crowned Sparrow (*Zonotrichia leucophrys oriantha*): a selected or incidental trait? *Auk* 102: 781-792.
- MOCK, D. W., & B. J. PLOGER. 1987. Parental manipulation of optimal hatch asynchrony in Cattle Egrets: an experimental study. *Anim. Behav.* 35: 150-160.
- MONAGHAN, P., J. D. UTTLEY, M. D. BURNS, C. THAINE, & J. BLACKWOOD. 1989. The relationship between food supply, reproductive effort and breeding success in Arctic Terns *Sterna paradisaea*. *J. Anim. Ecol.* 58: 261-274.
- MORRIS, R. D., R. A. HUNTER, & J. F. McELMAN. 1976. Factors affecting the reproductive success of Common Tern (*Sterna hirundo*) colonies on the lower Great Lakes during the summer of 1972. *Can. J. Zool.* 54: 1850-1862.
- , & D. A. WIGGINS. 1986. Ruddy Turnstones, Great Horned Owls, and egg loss from Common Tern clutches. *Wilson Bull.* 98: 101-109.
- NISBET, I. C. T. 1973. Courtship-feeding, egg-size and breeding success in Common Terns. *Nature* 241: 141-142.
- . 1978. Dependence of fledging success on egg-size, parental performance and egg-composition among Common and Roseate terns, *Sterna hirundo* and *S. dougallii*. *Ibis* 120: 207-215.
- , & M. E. COHEN. 1975. Asynchronous hatching in Common and Roseate terns, *Sterna hirundo* and *S. dougallii*. *Ibis* 117: 374-379.
- , & W. H. DRURY. 1972a. Measuring breeding success in Common and Roseate terns. *Bird-Banding* 43: 97-106.
- , & ———. 1972b. Post-fledging survival in Herring Gulls in relation to brood-size and date of hatching. *Bird-Banding* 43: 161-172.
- , J. M. WINCHELL, & A. E. HEISE. 1984. Influence of age on the breeding biology of Common Terns. *Colon. Waterbirds* 7: 117-126.
- O'CONNOR, R. J. 1978. Brood reduction in birds: selection for fratricide, infanticide and suicide? *Anim. Behav.* 26: 79-96.
- PARKES, K. C., A. POOLE, & H. LAPHAM. 1971. The Ruddy Turnstone as an egg predator. *Wilson Bull.* 83: 306-308.
- PARSONS, J. 1976. Factors determining the number

- and size of eggs laid by the Herring Gull. *Condor* 78: 481-492.
- , G. CHABRZYK, & N. DUNCAN. 1975. Effects of hatching date on post-fledging survival in Herring Gulls. *J. Anim. Ecol.* 45: 667-675.
- PIEROTTI, R., & C. A. BELLROSE. 1986. Proximate and ultimate causation of egg size and the "third-chick disadvantage" in the Western Gull. *Auk* 103: 401-407.
- QUINN, J. S., & R. D. MORRIS. 1986. Intraclutch egg-weight apportionment and chick survival in Caspian Terns. *Can. J. Zool.* 64: 2116-2122.
- RAHN, H., C. V. PAGANELLI, I. C. T. NISBET, & G. C. WHITTOW. 1976. Regulation of incubation water loss in eggs of seven species of terns. *Physiol. Zool.* 49: 245-259.
- SAFINA, C., J. BURGER, M. GOCHFELD, & R. H. WAGNER. 1988. Evidence for prey limitation of Common and Roseate tern reproduction. *Condor* 90: 852-859.
- SHAW, P. 1985. Brood reduction in the Blue-eyed Shag *Phalacrocorax atriceps*. *Ibis* 127: 476-494.
- SKAGEN, S. K. 1987. Hatching asynchrony in American Goldfinches: an experimental study. *Ecology* 68: 1747-1759.
- . 1988. Asynchronous hatching and food limitation: a test of Lack's hypothesis. *Auk* 105: 78-88.
- SKIPNES, K. 1983. Incubation behaviour of the Arctic Tern *Sterna paradisaea*, in relation to time of day and stage of incubation. *Ardea* 71: 211-215.
- SLAGSVOLD, T. 1982. Clutch size, nest size, and hatching asynchrony in birds: experiments with the Fieldfare (*Turdus pilaris*). *Ecology* 63: 1389-1399.
- , J. SANDVIK, G. ROFSTAD, O. LORENTSEN, & M. HUSBY. 1984. On the adaptive value of intra-clutch egg-size variation in birds. *Auk* 101: 685-697.
- SNEDECOR, G. W., & W. G. COCHRAN. 1980. *Statistical methods*. Ames, Iowa State Univ. Press.
- STOKLAND, J. N., & T. AMUNDSEN. 1988. Initial size hierarchy in broods of the Shag: relative significance of egg size and hatching asynchrony. *Auk* 105: 308-315.
- THOMPSON, S. C., & D. G. RAVELING. 1987. Incubation behavior of Emperor Geese compared with other geese: interactions of predation, body size, and energetics. *Auk* 104: 707-716.
- VERBEEK, N. A. M. 1988. Differential predation of eggs in clutches of Glaucous-winged Gulls *Larus glaucescens*. *Ibis* 130: 512-518.
- WARD, J. G. 1973. Reproductive success, food supply, and the evolution of clutch size in the Glaucous-winged Gull. Ph.D. dissertation, Vancouver, Univ. of British Columbia.
- WERSCHKUL, D. F. 1979. Nestling mortality and the adaptive significance of early locomotion in the Little Blue Heron. *Auk* 96: 116-130.
- WIGGINS, D. A., & R. D. MORRIS. 1987. Parental care of the Common Tern *Sterna hirundo*. *Ibis* 129: 533-540.