

RELATIVE EFFECTS OF HATCHING ORDER, EGG-SIZE VARIATION, AND PARENTAL QUALITY ON CHICK SURVIVAL IN COMMON TERNS

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ABSTRACT.—I examined the relative importance of factors influencing chick survival in manipulated and natural broods of Common Terns (*Sterna hirundo*). In nonmanipulated broods of three (modal brood size), egg mass decreased with laying order, siblings hatched asynchronously, and chick survival declined with hatching order. The ratio of a chick's mass to that of its siblings, at the time of brood completion, explained the greatest portion of variation in chick survival in these broods and in manipulated broods in which survival also varied with hatching order. Hatching order was an important component of mass ratio at brood completion. Egg mass did not influence survival in these brood types. In contrast, egg mass was important in manipulated broods in which chicks hatched synchronously and in natural broods of two, for which hatching order did not affect survival. Parental quality, as indicated by the number of a chick's siblings that survived, also had a positive effect on chick survival that was more important than the negative effect of increasing brood size. Length of the incubation period was positively correlated with size of last-laid eggs. My data did not strongly support the brood-reduction hypothesis of hatching asynchrony and egg-size variation. A smaller egg may benefit the last-hatched chick by reducing hatching asynchrony. Received 20 May 1992, accepted 29 November 1992.

IN MANY LARID SPECIES, partial incubation begins after the first egg is laid, resulting in asynchronous hatching within the clutch. The last egg in the clutch is usually relatively small (reviewed by Slagsvold et al. 1984, Reid 1987). Survival is generally lowest for youngest siblings in broods of terns (Langham 1972, Quinn and Morris 1986, Bollinger et al. 1990) and gulls (Parsons 1975a, Lundberg and Väisänen 1979). This decreased survival may be due to later hatching and to smaller egg size (Parsons 1970, 1975a, Nisbet 1973, 1978, Lundberg and Väisänen 1979). Larid-chick survival may also reflect the "quality" of parents (Coulson and Porter 1985, Bolton 1991, Sydeman and Emslie 1992), or timing of nesting (Parsons 1975b, Pierotti 1982). These and other factors are often interrelated (Nisbet 1973, Thomas 1983, Sydeman and Emslie 1992), thus complicating our understanding of their effects on chick survival. Although a few experimental studies of gulls have examined the relative effects of various factors on chick survival (Parsons 1975a, Hunt and Hunt 1976, Bolton 1991), similar work with terns is scarce (Nisbet 1978).

The reproductive benefits of hatching asynchrony and egg-size variation are not well understood for larids (Reid 1987, Bollinger et al. 1990) or for birds in general (Clark and Wilson 1981, Skagen 1987, Amundsen and Stokland 1988, Magrath 1990). Hatching order is generally more important than variation in egg or hatching size in establishing initial size hierarchies within broods (e.g. Bancroft 1984, Stokland and Amundsen 1988, Magrath 1992). However, it seems more important to ask how these factors influence chick survival itself (as in Parsons 1975a).

In Common Terns (*Sterna hirundo*), egg mass is lower for last-laid "C-eggs" than for "A-" or "B-eggs" in the modal three-egg clutch (Nisbet and Cohen 1975, this study). Siblings hatch asynchronously over a period of one to three days, and survival is lower for last-hatching C-chicks than for their older siblings (Langham 1972, Bollinger et al. 1990). Most chick mortality occurs within the first 7 to 10 days after hatching (Langham 1972, Nisbet and Drury 1972). I recorded chick survival in a population of Common Terns where starvation appeared to be the major cause of chick mortality and where predation on chicks did not occur. My objectives were to evaluate the relative importance of several variables (e.g. hatching order, egg mass, difference in mass among siblings, parental

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quality) as they influenced chick survival in normal and experimentally manipulated broods, and to relate these effects to hypotheses explaining intraclutch variation in egg size and chick survival.

METHODS

Field techniques.—I studied Common Terns breeding on Oneida Lake in Oswego County, New York, during 1983–1985. Approximately 350 pairs of terns nested on two small (0.046 and 0.120 ha), rocky shoals. Nests were checked daily during the egg-laying period in 1983–1984. I marked each egg with waterproof ink and weighed most eggs within 24 h of laying with a 50-g Pesola scale. All other eggs in 1983 and 1984 were weighed twice at a 7- to 10-day interval and the initial mass determined as in Rahn et al. (1976). I examined factors influencing chick survival in 1984–1985. During the hatching periods I checked each nest one to three times daily for new chicks, with an average interval between nest checks of $14.6 \pm \text{SD of } 7.9$ h. I weighed each chick at hatching and banded it with a U.S. Fish and Wildlife Service aluminum leg band. I also reweighed older siblings at the time of hatching of each chick.

To aid in recapture of chicks, in 1984 I enclosed groups of nests with 0.4-m-high wire-mesh and cloth fences (cf. Nisbet and Drury 1972). I weighed each chick within its enclosure every one to two days until days 11 to 14. In 1985, when no enclosures were used, the area around each nest was searched daily until the chicks reached day 10. Subsequently, I made four (1984) and three (1985) 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). Common Tern chicks can fledge (fly) as early as 22 days of age (Nisbet and Drury 1972). I considered chicks alive at day 18 or later in 1984 to have survived, as some chicks were able to escape from the enclosures prior to fledging. In 1985 I considered chicks alive at day 10 or later to have survived, as previous work in this colony indicated that more than 90% of all chick mortalities occurred by this age (Bollinger 1988).

Brood types studied.—I studied nonmanipulated, asynchronously hatching (“asynchronous”) broods of three chicks (1984, $n = 35$ broods; 1985, $n = 15$) and two chicks (1984, $n = 29$). I created synchronously hatching (“synchronous”) broods by placing together three randomly selected chicks hatching within 12 h ($\geq 70\%$ of broods) to 20 h of one another in 1984 ($n = 20$), and within 24 h of one another in 1985 ($n = 15$). Chicks were transferred when first found, within 14 h ($\geq 66\%$ of chicks) to 24 h after hatching. Only parents that laid three eggs were given synchronous broods. No deaths had occurred among chicks in asynchronous three-chick broods when first found on

the day of hatching. I created 20 “residual” broods of three chicks ($n = 14$) and two chicks ($n = 6$) in 1984 when normal broods were disrupted to form synchronous broods. These manipulated broods were similar to naturally occurring asynchronous three-chick broods in several attributes (see Results). Lastly, in 18 three-egg clutches in 1984 I removed the first or second egg or chick prior to hatching of the C-egg (Bollinger et al. 1990). In these broods, none of the variables I tested significantly affected chick survival (see below), so they were included only when all chicks were combined. I studied chicks hatching between 15 June–21 July 1984 and 17 June–11 July 1985. Approximately 93% of all chicks hatched within the sampling period in 1984 and 47% in 1985, although chicks continued to hatch into August. Hatching date did not appear to influence chick survival (see Results).

Statistical methods.—I used stepwise logistic-regression techniques (Harrell 1986) to evaluate the relative importance of variables to chick survival (Table 1; for use of logistic-regression analysis in ecological studies, see Bolton 1991). Only variables explaining a significant ($P < 0.05$) amount of variation were included in regression models. To avoid spurious correlations with the dependent variable, model building was stopped when the overall X^2 -statistic for testing all candidate variables jointly (residual X^2) had a P -value greater than 0.10, as suggested by Harrell (1986). I used the fraction of concordant pairs of observations, including one-half the number of tied pairs, to evaluate each logistic regression model (as in Schlinger and Adler 1990). This is calculated by considering all possible pairs of observations with different values of the dependent variable. Concordant pairs are those for which the observation with the larger value of the dependent variable has a higher predicted probability than does the other observation. This statistic is considered more reliable than a classification table for assessing the predictive ability of the model (Harrell 1986).

I combined all chicks for analysis and also grouped chicks both by brood type (e.g. asynchronous three-chick broods) and by “chick class” (i.e. by hatching order within a brood type). Synchronous chicks were treated as a single chick class to facilitate comparisons with chick classes in other brood types, as hatching intervals were minimized in these broods. Hatching order variables were omitted when synchronous chicks were included in analyses. Because egg variables were not recorded in 1985, hatching mass variables were substituted in 1985 for the corresponding egg mass variables.

As with any variable-selection procedure, logistic-regression analysis can erroneously omit variables from the final model due to stochastic variation and/or experimental error, especially if they are highly correlated with variables selected for the model. To examine this possibility, I looked at each independent variable that was highly correlated (i.e. $P < 0.005$)

TABLE 1. Definitions of variables of potential importance to Common Tern chick survival.

Egg mass.—Egg mass (g).
Hatch mass.—Hatching mass (g).
Mass ratio.—Mass ratio at brood completion (chick's mass divided by mass of largest chick in brood when last chick hatches or is added to brood).
Clutch mass.—Total mass (g) of parents' or adoptive parents' clutch.
Brood mass.—Total hatching mass (g) of brood.
Egg range.—Absolute value of difference (g) between egg mass and that of closest egg mass in clutch or adopted clutch.
Hatch range.—Absolute value of difference (g) between hatching mass and that of closest hatching mass in brood.
Lay order.—Laying order within original clutch; values increase as laying progresses.
Hatch order.—Hatching order within brood; values increase as hatching progresses; no value for synchronous chicks.
Hatch interval.—Absolute value of hatching interval (days) to nearest sibling; value zero for synchronous chicks.
Brood size.—Number of chicks in brood.
No. surviving.—Number of chick's siblings that survive to day 18 in 1984, or to day 10 in 1985.
Hatch date.—Hatching date.

with the dependent variable. If this variable also was highly correlated with the first variable selected, it could have been erroneously omitted from the model (for a similar analysis, see Frederick and Collopy 1989).

My data indicated that chicks within a brood were not entirely independent of one another (see Results). However, several trends appeared to justify those logistic-regression analyses which included chicks from the same brood. In the brood type for which I had the largest sample (asynchronous three-chick broods), results were similar when only one chick per brood was included (i.e. chicks grouped by chick class) and when all chicks were combined (i.e. grouped by brood type). Furthermore, survival generally varied with hatching order within a brood, indicating some independence among siblings. Although differences in hatching interval were minimized in synchronous broods, siblings had hatched in different nests; thus, variation among siblings was increased. Furthermore, I randomly selected one chick in each synchronous brood and examined trends in survival related to the variables of interest. Trends were similar to those shown by logistic regression in the more inclusive sample (for a similar analysis, see Skagen 1987).

Subsequent to logistic regressions I used chi-square tests, two-tailed *t*-tests, and Mann-Whitney *U*-tests to compare chicks that survived with those that died in terms of the variables evaluated in logistic regressions. I also used Spearman's correlation analyses to examine relationships among variables and chi-square analyses to compare chick survivorship within and

among broods. I considered differences between groups significant when $P < 0.05$.

RESULTS

Three-egg clutches represented 70% and two-egg clutches 22% of all clutches ($n = 313$). Egg mass decreased as each egg was laid in both two-egg (paired $t = 3.92$, $P < 0.001$, $n = 78$ clutches) and three-egg clutches ($n = 235$), but differences were small. In three-egg clutches, C-eggs ($\bar{x} = 20.4 \pm 1.6$ g) averaged 4.2% less than A-eggs (21.3 ± 1.6 g; paired $t = 9.16$, $P < 0.001$) and 3.3% less than B-eggs (21.1 ± 1.4 g; $t = 7.82$, $P < 0.001$), whereas B-eggs averaged 0.9% less than A-eggs ($t = 2.87$, $P = 0.005$). Egg mass was correlated with hatching mass (Pearson's $r = 0.83$, $P < 0.001$, $n = 225$).

In three-egg clutches, laying intervals were similar between the A- and B-eggs ($\bar{x} = 1.9 \pm 0.8$ days), and the B- and C-eggs (1.8 ± 0.6 days; $n = 118$). However, the interval between hatching of the A- and B-chicks ($\bar{x} = 0.7 \pm 0.6$ days) was less than that between the B- and C-chicks (1.2 ± 0.7 days; $n = 50$). This reflected the pattern of incubation onset. Clutches were incubated, on average, 66% of the time when only the A-egg was present, but incubation constancy increased to 88% with the laying of the B-egg and 93% with the C-egg (Bollinger et al. 1990). For chicks whose eggs were known (83% of chicks), eggs hatched in the order in which they were laid (Spearman's $r_s = 0.98$, $P < 0.001$, $n = 102$). Asynchronous three-chick broods hatched over a period of one to three days, with a mean interval of 1.9 ± 0.8 days ($n = 50$). Hatching intervals averaged 1.6 ± 0.9 days for residual broods ($n = 19$), 1.2 ± 1.1 days for asynchronous two-chick broods ($n = 29$), and 0.5 ± 0.5 days for synchronous broods ($n = 35$). No synchronous broods hatched over a period greater than one day.

In asynchronous three-chick broods, C-chicks survived significantly less often than did A- or B-chicks, and C-chicks in residual broods survived less often than did A- and B-chicks combined (Table 2). However, in asynchronous two-chick broods survival was similar for A- and B-chicks (Table 2). Synchronous broods were more successful ($\bar{x} = 2.2 \pm 0.9$ fledged/brood, $n = 33$ broods) than asynchronous three-chick broods (1.7 ± 1.0 , $n = 48$; Mann-Whitney $Z = 2.17$, $P = 0.03$; 1984 and 1985 combined). Survival did not differ between years ($X^2 = 0.01$,

TABLE 2. Survival rates and mass ratios at brood completion of Common Tern chicks grouped by brood type and chick class. Sample sizes in parentheses.

| Chick class | Percent survival ^a | Mass ratio ($\bar{x} \pm SD$) ^b |
|--|-------------------------------|--|
| Asynchronous three-chick broods | | |
| A | 72.9 (48) ¹ | 0.99 \pm 0.03 (43) ¹ |
| B | 60.4 (48) ¹ | 0.85 \pm 0.11 (44) ² |
| C | 36.0 (50) ² | 0.65 \pm 0.15 (50) ³ |
| A + B + C | 56.1 (148) | 0.83 \pm 0.18 (146) |
| Residual broods | | |
| A | 85.0 (20) | 0.95 \pm 0.13 (14) ¹ |
| B | 83.3 (18) | 0.88 \pm 0.13 (14) ² |
| C | 50.0 (14) ¹ | 0.72 \pm 0.08 (10) ³ |
| A + B | 84.2 (38) ² | 0.92 \pm 0.13 (28) |
| A + B + C | 75.0 (52) | 0.85 \pm 0.15 (42) |
| Asynchronous two-chick broods | | |
| A | 67.9 (28) ¹ | 1.00 \pm 0.00 (21) ¹ |
| B | 60.0 (25) ¹ | 0.85 \pm 0.12 (24) ² |
| A + B | 63.2 (57) | 0.93 \pm 0.11 (55) |
| Synchronous broods | | |
| — | 72.8 (103) | 0.93 \pm 0.07 (105) |

^a Different superscripts indicate different survival rates within brood types ($X^2 > 5.85$, $P < 0.025$, $df = 1$); same superscripts indicate $X^2 < 1.69$, $P > 0.10$, $df = 1$. Samples too small to compare separately A- or B-chicks with C-chicks in residual broods.

^b Different superscripts indicate different mass ratios within brood types (Mann-Whitney $Z > 2.47$, $P < 0.025$).

$df = 1$, $P > 0.90$) in asynchronous three-chick (1984, 56.3%, $n = 103$ chicks; 1985, 55.6%, $n = 45$) or synchronous broods (1984, 72.4%, $n = 58$; 1985, 73.3%, $n = 45$). Starvation appeared to be the major source of chick mortality. No evidence of predation was noted, and most chicks that died grew more slowly than those that survived (Bollinger et al. 1990).

Mass ratio, asynchrony, and parental quality.—When all chicks in 1984 were combined for logistic-regression analysis, variation in chick survival was best explained by mass ratio at brood completion (mass of a chick relative to that of its largest sibling at time of brood completion), the number of a chick's siblings that survived, and brood size, in that order (Table 3). When hatching order was included as a candidate variable by omitting synchronous chicks, hatching order, number of siblings surviving, and mass ratio were selected as the significant variables (Table 3). In these models the probability of chick survival increased with increasing mass ratio and number of siblings surviving, decreasing brood size, and earlier hatching within the brood.

Similarly, in asynchronous three-chick broods

(A-, B-, and C-chicks combined), variation in chick survival was best explained by mass ratio at brood completion and number of siblings surviving, in that order (Table 3). When chick classes were examined separately, the number of siblings surviving was the only significant variable for A- or B-chicks, but both mass ratio and number of siblings surviving were important for C-chicks (Table 4). Mass ratio was the only significant variable in residual broods (Table 3). However, hatching order may have been erroneously omitted as a significant variable in either of these brood types due to high correlations ($r_s > 0.79$, $P < 0.001$) between mass ratio and hatching order. In contrast to these brood types, mass ratio did not influence survival in asynchronous two-chick or synchronous broods (see below). In two-chick broods, the number of siblings surviving, followed by laying order, were selected as the important variables (Table 3).

Univariate tests also showed that the mean mass ratio at brood completion was higher for chicks that survived than for those that died when all chicks in 1984 were combined (Table 5), for chicks in asynchronous three-chick and residual broods (Table 5), and for C-chicks in asynchronous three-chick broods (Table 6). However, mass ratio did not differ between chicks that survived and those that died in synchronous broods or asynchronous two-chick broods, whether chicks were grouped by brood type or by chick class (Mann-Whitney U -tests, all $P > 0.50$ in 1984, $P > 0.10$ in 1985). A chick's chances of surviving were higher if its siblings survived than if they died ($X^2 > 4.64$, $df = 1$, $P < 0.05$) for A-, B-, and C-chicks in asynchronous three-chick broods ($n = 47$, 47, and 48, respectively), synchronous chicks ($n = 99$), and A- and B-chicks in asynchronous two-chick broods ($n = 24$ and 24).

The mean mass ratio was lower in asynchronous three-chick broods than in synchronous or asynchronous two-chick broods (Mann-Whitney $Z > 3.47$, $P < 0.001$), but did not differ between asynchronous three-chick and residual broods ($Z = 0.46$, $P = 0.65$; Table 2). Within asynchronous three-chick broods, mass ratio was significantly lower for C-chicks than for A- or B-chicks (Table 2). Mass ratio in the latter broods was more highly correlated with hatching order ($r_s = -0.82$, $P < 0.001$, $n = 146$) than with hatching mass ($r_s = 0.41$, $P < 0.001$, $n = 140$) or egg mass ($r_s = 0.24$, $P = 0.022$, $n = 94$). Among

TABLE 3. Variables influencing survival of Common Tern chicks grouped by brood type^a. Variables listed in order of significance. A plus sign (+) indicates positive correlation with survival. Numbers under variables indicate partial correlation coefficients (*P*-values in parentheses).

| Year | No. chicks | Variables included in logistic-regression model (<i>P</i> < 0.05) | | | Fraction of pairs concordant |
|--|------------|---|----------------------------------|-------------------------------|------------------------------|
| Asynchronous three-chick broods | | | | | |
| 1984 | 86 | +Mass ratio 0.306 (<0.001) | +No. surviving 0.161 (0.025) | | 0.744 |
| 1985 | 36 | +No. surviving 0.355 (0.004) | +Mass ratio 0.283 (0.014) | | 0.884 |
| 84 + 85 | 132 | +Mass ratio 0.332 (0.000) | +No. surviving 0.288 (0.000) | | 0.811 |
| Residual broods^b | | | | | |
| 1984 | 32 | +Mass ratio 0.356 (0.015) | | | 0.830 |
| Asynchronous two-chick broods | | | | | |
| 1984 | 39 | +No. surviving 0.326 (0.007) | -Lay order -0.264 (0.019) | | 0.909 |
| All chicks combined^{b,c} | | | | | |
| 1984 | 235 | +Mass ratio 0.260 (0.000) | +No. surviving 0.199 (<0.001) | -Brood size -0.100 (0.025) | 0.742 |
| All except synchronous chicks^b | | | | | |
| 1984 | 189 | -Hatch order -0.170 (0.003) | +No. surviving 0.232 (<0.001) | +Mass ratio 0.095 (0.041) | 0.786 |

^a Variables evaluated in 1984: egg mass, lay order, hatch order, mass ratio, clutch mass, no. surviving; in 1985, 1984 + 1985: hatch mass, hatch order, mass ratio, brood mass, no. surviving.

^b Brood size added to variables evaluated.

^c Hatch order omitted from variables evaluated.

TABLE 4. Variables influencing survival of Common Tern chicks grouped by chick class^a. Variables listed in order of significance^b. A plus sign (+) indicates positive correlation with survival. Numbers under variables indicate partial correlation coefficients (*P*-values in parentheses).

| Chick class | Year | No. chicks | Variables included in logistic regression model (<i>P</i> < 0.05) | | Fraction of pairs concordant |
|--|---------|------------|--|---------------------------------|------------------------------|
| Asynchronous three-chick broods | | | | | |
| A | 84 + 85 | 38 | +No. surviving 0.255 (0.026) | | 0.744 |
| B | 84 + 85 | 39 | +No. surviving 0.283 (0.012) | | 0.730 |
| C | 84 + 85 | 46 | +Mass ratio 0.208 (0.033) | +No. surviving 0.177 (0.049) | 0.756 |
| Synchronous broods^c | | | | | |
| — | 1984 | 52 | +Egg mass 0.221 (0.025) | | 0.727 |
| — | 84 + 85 | 104 | +Hatch mass 0.166 (0.021) | | 0.668 |
| Asynchronous two-chick broods | | | | | |
| A | 1984 | 20 | +Egg mass 0.300 (0.034) | | 0.914 |

^a Variables evaluated in 1984: egg mass, egg range, hatch interval, mass ratio, no. surviving; in 1985, 1984 + 1985: hatch mass, hatch range, hatch interval, mass ratio, no. surviving.

^b No variables significant for 1984 or 1985 chicks in asynchronous three-chick broods, 1985 synchronous chicks, or B-chicks in asynchronous two-chick broods. Samples too small to test chicks in residual broods.

^c Hatch interval omitted from variables tested.

TABLE 5. Significant comparisons ($P < 0.05$), by brood type, of Common Tern chicks that died and those that survived^a. Data presented as $\bar{x} \pm SD$ (n).

| Year | Variable | Died | Survived | Absolute t or Z^b | P |
|--|-------------|----------------------|-----------------------|-----------------------|--------|
| Asynchronous three-chick broods | | | | | |
| 1984 | Mass ratio | 0.77 \pm 0.17 (41) | 0.90 \pm 0.13 (58) | 3.90 ^u | <0.001 |
| 1985 | Mass ratio | 0.70 \pm 0.21 (20) | 0.84 \pm 0.20 (25) | 2.26 ^u | 0.024 |
| 84 + 85 | Mass ratio | 0.75 \pm 0.18 (61) | 0.88 \pm 0.15 (83) | 4.55 ^u | <0.001 |
| Residual broods | | | | | |
| 1984 | Mass ratio | 0.71 \pm 0.14 (7) | 0.90 \pm 0.13 (31) | 2.68 ^u | 0.007 |
| Asynchronous two-chick broods | | | | | |
| 1984 | Egg mass | 20.4 \pm 1.7 (19) | 22.0 \pm 1.9 (30) | 2.97 ^t | 0.005 |
| 1984 | Clutch mass | 57.8 \pm 10.0 (20) | 50.2 \pm 10.9 (31) | 2.49 ^t | 0.016 |
| All chicks combined | | | | | |
| 1984 | Mass ratio | 0.83 \pm 0.16 (90) | 0.91 \pm 0.12 (186) | 4.42 ^u | <0.001 |
| 1984 | Egg mass | 20.7 \pm 1.6 (97) | 21.3 \pm 1.5 (188) | 2.75 ^t | 0.006 |

^a Variables evaluated in 1984: egg mass, mass ratio, clutch mass, hatch date; in 1985, 1984 + 1985: hatch mass, mass ratio, brood mass.

^b Superscript U indicates Mann-Whitney U -test; superscript t indicates t -test.

C-chicks in these broods, mass ratio was negatively correlated with hatching interval between the B- and C-chicks ($r_s = -0.44$, $P = 0.001$, $n = 50$).

Egg mass.—In contrast to chicks in asynchronous three-chick and residual broods, egg mass and hatching mass significantly influenced survival in regressions involving synchronous chicks (Table 4). Similarly, in asynchronous two-chick broods, egg mass was important when A-chicks were considered separately (Table 4). In these models chick survival increased with increases in egg or hatching mass.

Univariate comparisons also showed that mean egg mass was higher for chicks that survived than for those that died when all chicks in 1984 were combined, and among chicks in synchronous broods and asynchronous two-chick broods (Table 7). However, egg mass did not differ between chicks that survived and those that died in asynchronous three-chick or residual broods, whether chicks were grouped by brood type or by chick class (Table 7).

Relationships among variables.—When I removed variation in length of the incubation period due to laying date, year (1983 or 1984),

TABLE 6. Significant comparisons ($P < 0.05$), by chick class, of Common Tern chicks that died and those that survived^{a,b}. Data presented as $\bar{x} \pm SD$ (n).

| Chick class | Year | Variable | Died | Survived | Absolute t or Z^c | P |
|--|---------|-------------|----------------------|----------------------|-----------------------|-------|
| Asynchronous three-chick broods | | | | | | |
| C | 1984 | Mass ratio | 0.66 \pm 0.13 (22) | 0.76 \pm 0.12 (13) | 2.13 ^u | 0.033 |
| C | 84 + 85 | Mass ratio | 0.62 \pm 0.13 (32) | 0.70 \pm 0.16 (18) | 2.09 ^u | 0.036 |
| Synchronous broods | | | | | | |
| — | 1984 | Egg mass | 20.1 \pm 0.8 (16) | 20.9 \pm 1.3 (43) | 2.90 ^t | 0.006 |
| — | 1985 | Hatch mass | 15.2 \pm 1.6 (12) | 16.6 \pm 2.1 (33) | 2.06 ^t | 0.046 |
| — | 84 + 85 | Hatch mass | 14.9 \pm 1.4 (28) | 15.8 \pm 1.8 (76) | 2.42 ^t | 0.017 |
| Asynchronous two-chick broods | | | | | | |
| A | 1984 | Egg mass | 20.1 \pm 1.7 (9) | 22.7 \pm 1.5 (13) | 3.82 ^t | 0.001 |
| B | 1984 | Clutch mass | 60.4 \pm 9.8 (9) | 49.1 \pm 10.5 (11) | 2.46 ^t | 0.024 |

^a Variables evaluated in 1984: egg mass, egg range, mass ratio, clutch mass, hatch date; in 1985, 1984 + 1985: hatch mass, hatch range, mass ratio.

^b No variables significant for A- or B-chicks in asynchronous three-chick broods, or for C-chicks in residual or 1985 asynchronous broods. Samples too small to test A- or B-chicks in residual broods.

^c Superscript U indicates Mann-Whitney U -test; superscript t indicates t -test.

TABLE 7. Comparisons, by brood type and chick class, of egg masses of Common Tern chicks that died and those that survived in 1984. Data presented as $\bar{x} \pm SD$ (n).

| Chick class | Died | Survived | Absolute t | P |
|--|---------------------|----------------------|--------------|-------|
| Asynchronous three-chick broods | | | | |
| A | 21.7 \pm 1.6 (8) | 21.3 \pm 1.7 (21) | 0.51 | 0.614 |
| B | 21.0 \pm 1.8 (13) | 21.6 \pm 1.4 (15) | 1.11 | 0.278 |
| C | 20.8 \pm 1.8 (20) | 20.7 \pm 1.3 (13) | 0.21 | 0.832 |
| A + B + C | 21.1 \pm 1.8 (42) | 21.3 \pm 1.5 (54) | 0.73 | 0.469 |
| Residual broods^a | | | | |
| C | 20.7 \pm 1.6 (5) | 20.8 \pm 1.8 (5) | 0.08 | 0.941 |
| A + B + C | 20.4 \pm 1.6 (9) | 21.1 \pm 1.4 (37) | 1.30 | 0.201 |
| Asynchronous two-chick broods | | | | |
| A | 20.1 \pm 1.7 (9) | 22.7 \pm 1.5 (13) | 3.82 | 0.001 |
| B | 20.7 \pm 1.7 (10) | 21.0 \pm 2.3 (11) | 0.25 | 0.802 |
| A + B | 20.4 \pm 1.7 (19) | 22.0 \pm 1.9 (30) | 2.97 | 0.005 |
| Synchronous broods | | | | |
| — | 20.1 \pm 0.8 (16) | 20.9 \pm 1.3 (43) | 2.90 | 0.006 |
| All chicks combined | | | | |
| — | 20.7 \pm 1.6 (97) | 21.3 \pm 1.5 (188) | 2.75 | 0.006 |

^a Samples too small to test A- or B-chicks in residual broods.

and colony, incubation length of C-eggs was positively related to egg mass ($r_s = 0.27$, $P = 0.017$, $n = 73$). Using all dates in 1984 for which data on eggs were available (i.e. through 25 June; 96% of three-egg clutches had been initiated by this date), laying date of the C-egg was negatively correlated with mass ratio of the C-chick ($r_s = -0.52$, $P = 0.003$, $n = 31$). However, there were no differences in hatching date between chicks that survived and those that died for any brood type or chick class in 1984, the year in which I sampled chicks hatching throughout most of the season (Mann-Whitney U -tests, $P > 0.05$; mean P -value of 12 tests = 0.37), or when all chicks were combined for this year ($Z = 0.82$, $P = 0.41$, $n = 305$). Hatching date also did not influence chick survival when I used logistic-regression analysis to evaluate an expanded set of variables for asynchronous three-chick broods and for all chicks combined in 1984 (Bollinger 1988).

I looked for trends in variables related to mass of three-egg clutches. To reduce the possibility of spurious correlations among variables due to correlations with laying date (above), I used data only from the major periods of clutch initiation (prior to 14 June each year). Clutch mass was not significantly associated with mass of the C-egg relative to clutch mass (1983, $r_s = 0.03$, $P = 0.754$, $n = 86$; 1984, $r_s = -0.03$, $P = 0.791$, $n = 116$) or with laying interval between the A- and C-eggs (1983, $r_s = -0.09$, $P = 0.411$, $n =$

80; 1984, $r_s = -0.04$, $P = 0.685$, $n = 86$). A suggestive, albeit nonsignificant, relationship was found to mass ratio of the C-chick at brood completion ($r_s = 0.37$, $P = 0.061$, $n = 27$).

DISCUSSION

Mass ratio, hatching order, and egg mass.—Mass ratio at brood completion was, in general, the most important variable influencing chick survival in the common naturally occurring brood type (asynchronous three-chick broods) and, specifically, among C-chicks in these broods. At the time the C-chick hatched, its mass averaged only 65% that of its largest sibling. Similarly, Morris et al. (1991) found that mass at brood completion was significantly lower for C-chicks in Common Tern broods than for A- or B-chicks.

The variable "mass ratio at brood completion" was constructed as an index of the chick's competitive ability relative to that of its siblings. Mass ratio was significantly correlated with hatching order, hatching mass, and egg mass. However, mass ratio was often selected instead of these variables in logistic regressions, suggesting that the combination of variables embodied by mass ratio was more important than any of the individual variables. Hatching order had a greater influence than egg or hatching mass in determining the effect of mass ratio on chick survival. Mass ratio was more highly correlated with hatching order than with either

mass variable. Hatching order was selected first in logistic-regression analysis when I combined all chicks except synchronous chicks, for which differences in hatching order did not exist. In the latter brood type, mass ratio was least variable and was not important in chick survival.

Mass ratio at brood completion, thus, was important in both brood types in which survival varied significantly with hatching order: asynchronous three-chick broods and manipulated, residual broods. Mass ratios were relatively low and variable in these brood types, and egg mass did not influence survival. In contrast, egg and/or hatching mass (but not mass ratio) affected chick survival only in those brood types in which differences in hatching order did not exist (synchronous broods), or in which hatching order did not affect survival (asynchronous two-chick broods; see below). In these brood types, egg mass may have influenced chick survival through effects on the mass, skeletal size, or condition of hatchlings (see Parsons 1970, Bolton 1991), or by influencing growth rate.

Similarly, relative size at brood completion was a better predictor of survival in nonmanipulated, asynchronous Jackdaw (*Corvus monedula*) broods than was absolute size at brood completion, although these variables were equally important in manipulated, synchronous broods (Gibbons 1987). Parsons (1970) and Lundberg and Väisänen (1979) demonstrated effects of both hatching order and egg size on chick survival in gulls. However, Parsons' (1975a, 1976) results indicated that hatching order was more important than laying order (i.e. egg size; see also Quinn and Morris 1986).

Like my study, several studies have found that egg or hatching size had limited or equivocal effects on chick survival in terns (Severinghaus 1983, Quinn and Morris 1986) and gulls (Davis 1975, Schreiber et al. 1979, Bolton et al. 1992). Sydeman and Emslie (1992) showed that egg size had little effect on Western Gull (*Larus occidentalis*) chick survival after controlling for correlated variables such as parental age. Survival increased with egg or hatching size when chicks were grouped by laying or hatching order in other studies of terns (Nisbet 1973, Feare 1976) and gulls (Parsons 1970, Lundberg and Väisänen 1979, Hébert and Barclay 1986), although, in general, parental attributes were not considered. However, chick survival was related to egg size even when researchers controlled for effects of parental quality in Common Terns

(Nisbet 1978) and Lesser Black-backed Gulls (*L. fuscus*; Bolton 1991). In the latter study, hatching order did not influence fledging rate, but the pattern of chick mortality appeared anomalous. In addition, egg size affected survival independently of parental age in Black-legged Kittiwakes (*Rissa tridactyla*; Thomas 1983), although hatching order was not held constant.

Parental quality and brood size.—Several studies of larids have indicated effects of differences in quality of the parents on chick survival (Nisbet 1973, Coulson and Porter 1985, Morris 1987). Both the quality (Bolton 1991) and age (Sydeman and Emslie 1992) of parents were more important than egg size in influencing chick survival among gulls, although other studies examining these variables gave somewhat conflicting results (Nisbet 1978, Thomas 1983). My results showed that number of siblings surviving was second only to mass ratio in influencing chick survival in asynchronous three-chick broods and when all chicks were combined. This variable probably reflected the parents' ability to tend their young, as chicks survived more often when their siblings survived. Thus, benefits gained by having high-quality parents may partially override disadvantages due to competition from surviving siblings. When chick classes in asynchronous three-chick broods were examined separately, number of siblings surviving was the only significant variable for A- or B-chicks, which had consistently high mass ratios. In contrast, mass ratios were lower and more variable for C-chicks. Although a C-chick had a higher chance of surviving if its siblings also survived, its competitive stature appeared more important than the quality of its parents.

Similarly, number of siblings surviving, followed by laying order, were important when chick classes were combined in asynchronous two-chick broods. In these broods mass ratios were consistently high. Survival was either very high or very low for both siblings, depending on the original clutch size and the laying order of the egg, if any, that failed to hatch (Tables 5 and 6; Bollinger 1988). Both of these factors probably reflect parental performance.

Larger brood sizes were associated with lower survival rates per chick when all chicks in 1984 were combined (as in Thomas 1983; but see Parsons 1975b); however, brood size was less important than number of siblings surviving. Again, this suggests that parental quality can be more important than sibling competition in

influencing survival (see also Langham 1972, Coulson and Porter 1985). Lower average survival rates in larger broods resulted both from low survival of C-chicks and from decreased survival of B-chicks (60%) when C-chicks hatched, compared with broods in which C-eggs were not laid or, if laid, did not hatch (88%; Bollinger 1988). The latter represents an actual brood-size effect, as also noted by Hébert and Barclay (1986).

Adaptive significance of intraclutch variation.— Given the potential effects on chick survival of both hatching asynchrony and egg size, the common pattern for egg size to decrease with hatching order in larids may be consistent with a "brood-reduction" strategy (Nisbet and Cohen 1975, Clark and Wilson 1981). According to the brood-reduction hypothesis (Lack 1954), hatching asynchrony is an adaptation to produce a competitive hierarchy within the brood, which may be accentuated by egg-size variation (Slagsvold et al. 1984). This hierarchy maximizes overall brood success by facilitating death of the youngest sibling when food resources are low. However, my results concerning the role of egg-size variation in a brood-reduction strategy were equivocal. First, egg size only influenced chick survival in those brood types in which hatching asynchrony was not important, and had no effect on chick survival in non-manipulated broods of three (the most common brood size). This result probably reflected the small variation in egg size within clutches; C-eggs averaged only 4% less than A-eggs in mass. The brood-reduction hypothesis also predicts that parental and/or resource quality during the egg-laying period should be positively correlated with competitive attributes of the C-chick established by the parents at this time. Clutch mass can reflect parental quality (Bolton 1991) or food availability (Nisbet 1977). However, clutch mass was not significantly related to the relative mass of the C-egg, the interval between laying of the A- and C-eggs, or the mass ratio of the C-chick at brood completion.

Common Tern brood success was significantly higher in synchronous broods than in asynchronous broods. This suggests that brood reduction may not be the function of hatching asynchrony in this species (for reviews of similar findings in other species, see Skagen 1987, Amundsen and Stokland 1988; for another opinion, see Magrath 1990). Rather, hatching asynchrony may reflect constraints, such as egg

predation, during the egg-laying period (Bollinger et al. 1990). The reported effects of egg size on chick survival have varied among studies of larids, and other species have greater within-clutch variation in egg size than that reported here (reviewed by Reid 1987). However, my findings argue against the validity of viewing hatching asynchrony and egg-size variation as paired adaptations for brood reduction in Common Terns.

Parsons (1972, 1976) suggested that smaller egg size may increase, rather than decrease, the chances of survival of the last chick by reducing the degree of hatching asynchrony within the brood, if smaller eggs have shorter incubation periods. Incubation length was related to larid egg size in two studies (Parsons 1972, Nisbet and Cohen 1975), although not in others (Feare 1976, Schreiber et al. 1979). My data were consistent with Parson's hypothesis, as I observed a positive relationship between the size of the C-egg and the length of its incubation period. Hatching order appeared more important than egg size in influencing C-chick survival in this and Parsons' (1975a, 1976) studies. Therefore, positive effects of earlier hatching by small C-eggs may override any negative effects of small size at hatching.

Results of recent studies have suggested that variation in egg mass within larid clutches may reflect physiological constraints on the laying female (Pierotti and Bellrose 1986, Reid 1987, Sydeman and Emslie 1992), with C-egg size possibly affected by the onset of incubation of the A-egg and the resulting decrease in courtship feeding (Houston et al. 1983, Salzer and Larkin 1990). In Common Terns the clutch of three eggs represents a substantial investment by the female (45% of adult body mass; Wiggins and Morris 1987). Nisbet (1973) showed that courtship feeding by male Common Terns was related to the absolute size of C-eggs laid by their mates (but not to their relative size; Reid 1987). Similarly, courtship feeding in Glaucous-winged Gulls (*L. glaucescens*) was related to the relative size of C-eggs (Salzer and Larkin 1990). Furthermore, C-eggs were larger than normal relative to A- and B-eggs when Western Gulls had access to a superabundant food supply (Pierotti and Bellrose 1986) and when Glaucous-winged Gulls were given food supplements after clutch initiation (Reid 1987; for conflicting results, see Bolton et al. 1992).

My results indicated that intraclutch varia-

tion in egg size was small and that, in this population, egg size did not consistently influence chick survival. In contrast, the "quality" of a chick's parents and its mass relative to that of its siblings at brood completion were important in determining its chances of survival. The latter relationship was strongly influenced by hatching order. Although the small size of the C-egg may benefit the C-chick by reducing detrimental hatching asynchrony, the function, if any, of intraclutch variation in either egg size or hatching order is not clearly understood for this species.

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