

VARIATIONS IN GROWTH OF ROSEATE TERN CHICKS¹

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Abstract. We measured growth parameters of Roseate Tern (*Sterna dougallii*) chicks at two contrasting colonies: Bird Island, Massachusetts, and Falkner Island, Connecticut, from 1987 through 1990. Differences in growth parameters among individual chicks are used to explore differences in parental performance, whereas differences in average growth parameters among colonies and years are used to explore differences in average environmental conditions. Chicks were marked at hatching and weighed at one- or two-day intervals. For each chick that survived to fledging, we calculated two measures of growth: linear growth rate and asymptotic mass. There were no significant differences between growth parameters of first-hatched chicks in broods of one and two. Both measures of growth were significantly lower and more variable for second-hatched chicks than for first-hatched chicks. Both measures were significantly positively related to egg mass and negatively related to hatch date. After controlling for these variables, differences between colonies and among years were relatively small and inconsistent. Mean survival of second-hatched chicks was positively correlated with the mean growth rate of survivors across colonies and years. These findings are consistent with a general hypothesis that growth of chicks reflects individual parental performance and parental quality.

Key words: *Growth; variability; Roseate Tern; Sterna dougallii; Massachusetts; Connecticut.*

INTRODUCTION

Patterns of growth in bird chicks integrate information about evolutionary adaptations and about the performance of individual chicks or parents in relation to environmental factors (Ricklefs 1968, 1979). Differences in average growth patterns among species reflect adaptations to energetic constraints or to other ecological factors (Ricklefs 1979, 1983, 1992; O'Connor 1984). In contrast, variations in growth rates among individual chicks reflect variability in the environment or variations in individual performance. In species whose chicks feed themselves (e.g., waterfowl), variations in growth rates result mainly from variations in characteristics of the chicks (Brisbin et al. 1987a, Cooch et al. 1991, Sedinger and Flint 1991). In species whose chicks are fed by the parents (e.g., seabirds), variations in growth rates result primarily from variations in characteristics or quality of the parents (Furness 1983, Lequette and Weimerskirch 1990).

Patterns of average growth in seabird chicks have been reported for many species (e.g., Nelson 1978, Langham 1983, Ricklefs 1983, Warham 1990), but comparatively few studies have addressed variations among individuals. The most detailed study reported to date is that of Furness (1983), who reported differences in growth of individual Great Skua (*Catharacta skua*) chicks in relation to parental age, hatching date, egg volume, brood size, and hatching order. Furness did not actually measure growth rates. Instead, he used the deviation of each chick's mass from the average pattern for the colony as an index of "growth" for that individual chick.

Selection of a single measure to represent the growth of an individual chick is complicated by the nonlinear pattern of growth (Ricklefs 1968). Several authors have fitted data on chick growth to nonlinear sigmoid models and have used parameters of these models to characterize the growth of individual chicks (Barrett and Runde 1980, van Heezik 1990, Cruz and Cruz 1990). The parameters calculated in these studies, however, integrate information from different parts of the growth curve, and estimating them for

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individual chicks generally requires complete growth curves, which are often difficult to obtain. Other practical difficulties in growth-curve analysis have been discussed by Brisbin et al. (1987b) and Zach (1987). Some authors have used simpler measures to characterize the growth of individual chicks, such as the slopes of the linear or near-linear parts of the growth curves (Nisbet 1978, Coulson and Porter 1985) or the asymptotic masses (Brooke 1986, Lequette and Weimerskirch 1990). These measures are derived from different parts of the growth curve and may be influenced in different ways by environmental factors or individual performance (O'Connor 1984). Hence, it may be advantageous to calculate them separately, avoiding the confounding of effects that may result from logistic analysis.

This paper reports a study of factors associated with variations in growth of chicks of the endangered Roseate Tern (*Sterna dougallii*). We measured the growth of Roseate Tern chicks at two colonies in the northeastern United States in four consecutive years. Average growth curves for this species have been reported previously by LeCroy and Collins (1972), Langham (1983) and Nisbet (1981), and have been analyzed by Langham (1983) and Schew (1990). We weighed individually-marked chicks and calculated linear growth rate and asymptotic mass for each chick. We examined variations in these parameters in relation to location, year, hatch order, brood size, hatch date, and egg mass. We expected that variations in growth related to hatch date and egg mass would reflect differences in parental performance, whereas variations related to hatch order and brood size would reflect sibling competition. After controlling for these variables, we expected that variations in growth related to location and year would reflect variations in food availability or other environmental factors. We chose two contrasting colonies. These were a large, consistently productive colony and a smaller, usually less productive colony. We studied them for four years to investigate year-to-year differences. Our study was designed to investigate whether measurements of variations in chick growth could provide useful information on some or all of these factors. We hoped that information on factors limiting growth rates and productivity would contribute to management of this endangered species.

METHODS

We studied Roseate Terns at Bird Island, Massachusetts (41°40'N, 70°43'W), and Falkner Island, Connecticut (41°13'N, 72°39'W), a unit of the Stewart B. McKinney National Wildlife Refuge. These colony sites are referred to hereafter as BI and FI. The colony sites and their microhabitats were described by Nisbet et al. (1990) and Spendelow (1982), respectively. During the study period (1987–1990), BI supported about 1,600 pairs of Roseate Terns and FI supported about 160 pairs.

Study methods differed slightly between sites, because of differences in substrate, nest density, and behavior of chicks. At BI, between 150 and 210 nests (9–13% of the total) were selected for study. In each year, four or five study-plots of 50–100 m² were selected, including one or two central plots and three or four peripheral plots. The plots were selected to sample nests in different areas of the colony and in different substrates, although birds in more open areas and birds nesting late in the season were somewhat oversampled. At FI, almost all (95–100%) of the nests in the colony were studied in each year.

Study nests were marked when first found, usually at the time of laying, except that one plot in each year at BI was left undisturbed until the earliest nests were hatching. Otherwise, eggs were marked at laying, using a non-toxic, waterproof marker. About 60% of the eggs at BI were weighed, usually within five days of laying; the fresh mass of each egg was estimated (to within about ± 0.2 g) by back-calculating to the day of laying, using data on the average rate of loss of mass (Rahn et al. 1976, Nisbet 1981). At FI, no eggs were weighed in 1987; about 95% of the eggs laid in 1988–1990 were weighed, either on the day of laying or on the next day.

Nests were visited either daily or on alternate days at the time of hatching. Chicks were banded with an incoloy (nickel-chromium-steel alloy; Nisbet 1988) band at hatching and were weighed. In cases where nests were not checked daily (about 30% of nests), the date of hatching of each chick was assigned based on initial mass (usually 12–17 g on the day of hatching), the date of hatching of the other chick in the brood (usually three-day hatching interval between chicks), and/or the date of laying of one or both eggs (usual incubation period 23 days; Nisbet 1981). Based on

this information, we believe that the date of hatching was correctly assigned for at least 95% of chicks, and was in error by at most one day for the remainder. The day of hatching is denoted day 0; on average, chicks would have been about 0.5 days old on day 0, 1.5 days old on day 1, and so on.

“Hatch order” is defined as follows: A1, only chick in brood of one; A2, first chick in brood of two or more; A, either A1 or A2; B, second chick in brood of two or more. Although a few third chicks hatched, none survived more than five days. “Hatch date” is defined as the date of hatching of the A-chick (1 May = 1).

Chicks were searched for and weighed at regular intervals. At BI, most chicks sought cover under dense vegetation and were difficult to find; about half the broods moved out of the study-plots and were lost from the study, except that a few chicks were encountered occasionally elsewhere (up to 60 m from the location of hatching). Chicks were searched for daily for the first 3–5 days, then on alternate days until they disappeared or fledged. No predators were seen in the colony during the chick-raising period, and we found no evidence that any chicks were taken by predators (Nisbet et al. 1990). At FI, most nests were in artificial sites (automobile tires or nest boxes; Spendelov 1982). Many chicks remained in the tires until aged 15–25 days, but others dispersed into rocky areas where they were difficult to find; a few are believed to have been taken by predators in two years. Chicks were generally searched for daily.

Analysis in this paper is limited to chicks that are known or judged to have survived to fledging. Most chicks that died were B-chicks that failed to grow normally from the start and died within 5–8 days of hatching (Nisbet 1978, 1981, Nisbet et al. 1990). Very few of these chicks met the minimum criteria for calculation of growth parameters (see below); the few that did so showed low or negative growth rates and did not reach asymptotic masses.

Judgment of chick survival was often necessary because many chicks dispersed into dense cover and could not be followed to determine survival directly. Criteria for judging survival were given by Nisbet et al. (1990). We included in the study all chicks that were known to have survived to the age of at least five days and were within the normal range of masses for their age

when last encountered (categories F1 or F2 of Nisbet et al. 1990). We also included 21 chicks at FI that appeared to be growing normally but were taken by predators or died from accidental causes unrelated to growth. We excluded all chicks known or judged to have died (categories D1–D5 of Nisbet et al. 1990), and all chicks for which information was insufficient to determine survival (categories U1–U5 of Nisbet et al. 1990). We excluded a few chicks that were not encountered early enough to estimate the date of hatching, and seven chicks at BI whose rank within the brood is thought to have changed as a result of adoptions.

Average survival of chicks at each colony is estimated as the proportion of all chicks, for which outcomes are known, which are judged to have survived to fledging. Data on chick survival at BI were published by Nisbet et al. (1990: Method 2); data for FI were calculated by the same method.

All chicks were weighed using Pesola® or Avinet® spring balances. Small chicks were weighed on 30 g or 50 g balances, medium-sized chicks on 100 g balances, and large chicks on 300 g balances. Chicks were weighed to the nearest 0.1 or 0.2 g on days 0–2, to the nearest 0.5 or 1 g on days 3–13, and to the nearest 1 g after day 13. Chicks were weighed in plastic cones (BI) or plastic mesh bags (FI). Balances were calibrated at least once per season and were tared at regular intervals.

Quality control procedures included checking each weight in the field against the preceding sequence of weights for the same chick. Records that deviated from the normal pattern of growth were immediately re-checked, and a few errors (e.g., in weighing or in reading band numbers), were thereby detected and corrected. Errors that did not lead to deviations from the normal pattern of growth may have remained uncorrected, but such errors were probably rare and would not have affected the results of the analysis.

Because most chicks were not found daily or even at regular two-day intervals, it was not possible to fit data from each chick to a complete growth curve (Langham 1983, Schew 1990). Therefore, we defined two growth parameters that could be determined from incomplete or irregular data. “Linear growth rate” (LGR) is defined as the slope of a regression line fitted to mass data during the quasi-linear period of growth (3–

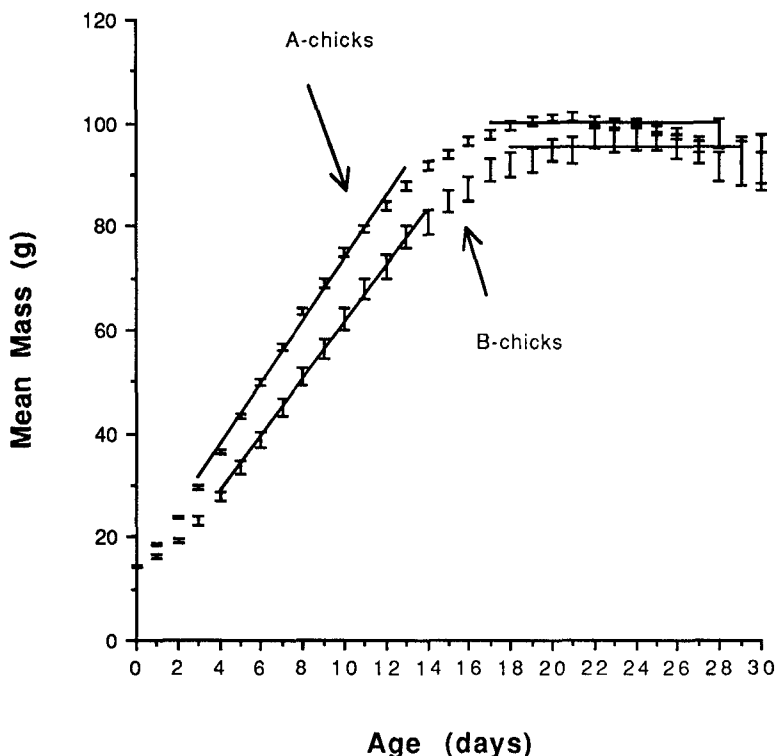


FIGURE 1. Composite growth data for A-chicks (upper curve, $n = 1,016$) and B-chicks (lower curve, $n = 274$) of Roseate Terns. Data from both colony sites and all four years are pooled. Vertical bars indicate ± 2 standard errors. The straight lines show the ranges over which the measures of growth for each chick were computed: left, LGR; right, AM. Mean values, standard deviations, and sample sizes for each day are listed in Appendix 1.

13 days for A-chicks, 4–14 days for B-chicks: Figure 1). LGR is calculated only for chicks with at least four data points within this period. “Asymptotic mass” (AM) is defined as the mean of all masses measured during the period of near-constant mass (17–28 days for A-chicks, 18–29 days for B-chicks: Figure 1). We also calculated the median mass during these periods and compared the results of statistical analyses using means and medians. Because the results of these analyses were virtually identical, we report results only for the mean. AM was calculated only for chicks with at least two data points within the periods specified.

As a result of long-term studies, Roseate Terns breeding at both FI and BI are habituated to human disturbance (Nisbet 1981), and we found no evidence that survival or growth of chicks was affected by our study activities. Although studies of other terns have indicated that growth rates may be affected by exposure to certain en-

vironmental contaminants (Harris et al. 1993), levels of these contaminants in Roseate Terns at FI and BI were very low when measured in 1981 (Custer et al. 1983). Accordingly, we assume that variations in growth rates measured at these locations reflect the influence of natural ecological factors only.

Statistical analyses were conducted using SAS (1985). We used analysis of variance (ANOVA) to analyze the dependence of LGR and AM on categorical variables (location, year, brood size, hatch order, and their interactions). Where ANOVA showed significant effects, Tukey’s multiple comparison procedure (hereafter, Tukey’s test) was used to assess the statistical significance of differences among categories. Bartlett’s test was used to test for inhomogeneity of variances of the residuals.

We used analysis of covariance (ANCOVA) to analyze the simultaneous effects of categorical and continuous variables (hatch date and egg

TABLE 1. Mean values of linear growth rate (g day⁻¹) grouped by year, location, and hatch order. Values tabulated are mean ± SE (sample size).¹

Year	Bird Island		Falkner Island	
	A-chicks	B-chicks	A-chicks	B-chicks
1987	6.06 ± 0.07 (112)a#	5.15 ± 0.34 (30)b*	6.09 ± 0.09 (97)a	6.44 ± 0.18 (23)a
1988	6.18 ± 0.12 (64)a#	4.70 ± 0.30 (9)b	5.93 ± 0.08 (125)a#	5.31 ± 0.13 (47)b
1989	6.54 ± 0.13 (52)a*	6.30 ± 0.17 (14)a*	5.69 ± 0.13 (93)a	5.02 ± 0.22 (24)b
1990	5.97 ± 0.10 (65)a	5.15 ± 0.30 (22)ab	5.96 ± 0.09 (106)a	5.57 ± 0.27 (24)ab

¹ a,b, Entries in the same column that share a letter are not significantly different; #, significantly different from B-chicks at the same location in the same year; *, significantly different from chicks of same hatch order at Falkner Island in the same year (all comparisons, $P < 0.05$, Tukey's test).

mass) on LGR and AW. The linear model was as follows:

$$\text{LGR}_{ijk} \text{ (or AM}_{ijk}) = C_{ijk} + H_{ijk} \text{ (hatch date)} \\ + E_{ijk} \text{ (egg mass)} + \text{error},$$

where i, j, k index hatch order, location, and year, respectively, C_{ijk} is an intercept term and H_{ijk} , E_{ijk} are regression coefficients. Initially, the model was run separately for each of the 14 combinations of i, j , and k . Reduced models (constraining parameters over various combinations of the categorical variables) were explored until the most parsimonious model consistent with the data was found. The criterion for rejection of a reduced model was $P < 0.05$ for the likelihood ratio F -test comparing the constrained parameters of the reduced versus the full model. ANCOVA was also used to analyze the dependence of egg mass on hatch date, hatch order, location and year. Pearson's correlation coefficient r or Spearman's rank correlation coefficient r_s were used to assess correlations between selected variables.

All analyses were performed on untransformed variables. Because of the large sample sizes, we expected that the parameter estimates that are compared in the ANOVAs and ANCOVAs would be approximately normally distributed, even though the dependent variables showed some deviations from normal distributions.

RESULTS

Our sample included mass data for 1,764 chicks, of which 1,290 were judged to have survived to fledging. Numbers that met the criteria for inclusion in the analysis were as follows: ANOVA for linear growth rate (LGR), $n = 907$; ANOVA for asymptotic mass (AM), $n = 737$; ANCOVA for LGR, $n = 673$; ANCOVA for AM, $n = 538$; ANCOVA for egg mass, $n = 1,268$. The average number of records per chick used in computing

the parameter estimates was 7.0 for LGR and 5.3 for AM.

All analyses were initially performed with hatch order categories A1 and A2 (A-chicks from broods of one and two) kept separate. None of the analyses showed any significant differences between these two categories ($P > 0.05$, results not shown). Accordingly, these two categories were merged in all subsequent analyses.

GROWTH CURVES FOR A- AND B-CHICKS

Figure 1 presents composite growth data for all A-chicks ($n = 1,016$) and B-chicks ($n = 274$) that survived to fledging. Summary statistics for each day of age are listed in Appendix 1. On average, B-chicks were significantly lighter on every day from day 0 through day 26 ($P < 0.01$, pairwise two-sample t -tests).

DEPENDENCE OF GROWTH ON HATCH ORDER, LOCATION, AND YEAR

Tables 1 and 2 present summary statistics for LGR and AM, respectively, and the results of ANOVAs. Both LGR and AM were more variable for B-chicks than for A-chicks (residual variances 1.474 and 0.850, respectively, for LGR; 83.45 and 37.42, respectively, for AM; $P < 0.0001$, Bartlett's tests). [Because of this inequality of variances, significance levels reported for subsequent tests under ANOVA and ANCOVA are only approximate.]

Linear growth rate depended strongly on hatch order ($F = 45.65$, $P < 0.0001$), but this result is difficult to interpret because of interactions among hatch order, location, and year (Table 1). The footnotes to Table 1 indicate the results of pairwise comparisons among the categories. Three of eight comparisons between A- and B-chicks (within years and locations) were significant. Four of 24 comparisons between years (within locations and hatch orders) were significant, all for B-chicks. Three of eight comparisons between

TABLE 2. Mean values of asymptotic mass (g) grouped by year, location, and hatch order. Values tabulated are mean \pm SE (sample size).¹

Year	Bird Island		Falkner Island	
	A-chicks	B-chicks	A-chicks	B-chicks
1987	100.4 \pm 0.9 (42)a	94.0 \pm 3.1 (17)ab	100.6 \pm 0.6 (82)a	98.1 \pm 1.1 (20)a
1988	103.2 \pm 0.8 (66)a#*	95.0 \pm 4.4 (11)ab	97.6 \pm 0.6 (103)ab	95.4 \pm 1.0 (45)a
1989	102.2 \pm 0.9 (51)a*	99.8 \pm 4.4 (18)a*	96.2 \pm 0.7 (80)b	90.9 \pm 2.1 (22)a
1990	100.3 \pm 0.7 (66)a#	90.4 \pm 2.2 (18)b	101.1 \pm 0.6 (76)a	97.5 \pm 1.7 (20)a

¹ a, b, Entries in the same column that share a letter are not significantly different; #, significantly different from B-chicks at the same location in the same year; *, significantly different from chicks of same hatch order at Falkner Island in the same year (all comparisons, $P < 0.05$, Tukey's test).

locations (within years and hatch orders) were significant, the most consistent difference being higher growth rates at BI than at FI in 1989.

Asymptotic mass depended strongly on hatch order ($F = 62.22$, $P < 0.0001$), but this result also is difficult to interpret because of interactions (Table 2). The footnotes to Table 2 indicate the results of pairwise comparisons among the categories. Two of eight comparisons between A- and B-chicks (within years and locations) were significant. Three of 24 comparisons between years (within locations and hatch orders) were significant, for B-chicks at BI and A-chicks at FI. Three of eight comparisons between locations (within years and hatch orders) were significant, the most consistent difference again being higher asymptotic masses at BI than at FI in 1989.

DEPENDENCE OF GROWTH ON HATCH DATE AND EGG MASS

Tables 3 and 4 present the results of ANOCOVAs for linear growth rate and asymptotic mass, respectively. For LGR, the most parsimonious model constrained the regression coefficients to

TABLE 3. Results of analysis of covariance (ANOCOVA) for linear growth rate (LGR).

Independent variable ¹	Regression coefficient	F	P
Hatch order	- ²	33.28	<0.0001
Egg mass	+0.070 ³	5.83	0.016
Hatch date	-0.011 ³	4.25	0.040
Year	- ⁴	4.25	0.0055
Year \times location	- ⁵	9.45	<0.0001

¹ In Tables 3–5, the only independent variables and interactions listed are those whose contributions to the model were statistically significant ($P < 0.05$).

² Contribution to intercept C_{ijk} was +0.33 g day⁻¹ (A-chicks > B-chicks), without significant interaction with year or location.

³ Regression coefficients were not significantly different among all values of the categorical variables.

⁴ Significant interaction with location.

⁵ The only combination of year with location yielding a significant contribution to the model was that of 1989 with BI (LGR higher at BI than at FI by 1.55 g day⁻¹; $F = 6.60$, $P < 0.01$).

be the same for all values of i , j and k . Both regression coefficients were significantly different from zero, with a positive dependence on egg mass and a negative dependence on hatch date (Table 3). As in the ANOVAs, LGR depended strongly on hatch order ($F = 33.28$, $P < 0.0001$), with no significant interactions. Year and location showed a significant interaction; the only combination that was individually significant was that of 1989 with BI ($P < 0.05$, see footnote to Table 3).

For asymptotic mass, the most parsimonious model constrained the regression coefficients on egg mass to be the same for all i , j and k ; the regression coefficients on hatch date were the same for all j and k , but were different for A-chicks and B-chicks. The regression coefficient on egg mass was positive and significant; that on hatch date for B-chicks was negative and significant; that on hatch date for A-chicks was not significantly different from zero (Table 4). The intercept term (C_{ijk}) is difficult to interpret because of multiple interactions among hatch order, location and year (Table 4).

RELATIONSHIP BETWEEN HATCH DATE AND EGG MASS

ANOCOVA using egg mass as the dependent variable and hatch date, year, location and hatch order as independent variables showed no significant relationship with any variable over the 538 cases used in the analysis for AM. The Pearson correlation coefficient between egg mass and hatch date within this data set was -0.0275 (not significantly different from zero, $P > 0.05$), justifying treating egg mass and hatch date as independent variables in the ANOCOVAs. However, ANOCOVA on the full data set ($n = 1,268$, including data for eggs that gave rise to chicks that did not survive to fledging) indicated that egg mass was significantly negatively related to

TABLE 4. Results of analysis of covariance (ANOCOVA) for asymptotic mass (AM).

Independent variable	Regression coefficient	F	P
Egg mass	+0.777	10.31	0.0014
Hatch date (B-chicks)	-0.358 ¹	10.31	0.0014
Hatch order	- ²	7.31	0.0071
Year × location	- ²	10.95	<0.0001
Location × hatch order	- ²	5.62	0.018
Year × location × hatch order	- ²	3.10	0.046

¹ Regression coefficient on hatch date for A-chicks was +0.044 (not significant). Regression coefficients were not significantly different among all values of year and location.

² Significant interactions with other variables.

hatch date among A-eggs, but not B-eggs (Table 5).

CORRELATION BETWEEN LINEAR GROWTH RATE AND ASYMPTOTIC MASS

The results in Tables 1–4 show similar patterns of variation in LGR and AM, and similar relationships of LGR and AM with the independent variables. Pearson's correlation coefficient between LGR and AM among individual chicks was +0.580 (significantly different from zero, $P < 0.0001$, $n = 610$).

RELATIONSHIP BETWEEN GROWTH AND SURVIVAL

Figure 2 shows the relationship between the average survival of B-chicks in each of the eight combinations of location × year and the corresponding average values of LGR for the surviving B-chicks. There is a significant positive correlation between these two variables ($r_s = 0.655$, $n = 8$, $P < 0.05$, one-tailed). The correlation between mean survival and the mean value of AM was not significant ($P > 0.05$). No similar relationship was found for A-chicks, because survival of A-chicks was uniformly high in all colony-years.

CORRELATION BETWEEN GROWTH OF A- AND B-CHICKS WITHIN BROODS

Within broods of two, there were significant correlations between A- and B-chicks for both LGR ($r = +0.262$, $n = 164$, $P < 0.001$) and AM ($r = +0.442$, $n = 138$, $P < 0.0001$).

DISCUSSION

In Roseate Terns, survival of A-chicks from hatching to fledging is uniformly high and constant (averaging 97% at BI and 90% at FI during this study), whereas survival of B-chicks is lower and much more variable, both within and among

years (Nisbet 1981, 1993, Nisbet et al. 1990, Burger et al. in press; Fig. 2). The results of this study show further that the growth rates and asymptotic masses of A-chicks were high and were unaffected by the presence of a younger sibling, whereas the growth rates and asymptotic masses of B-chicks were lower and were much more variable (Fig. 1, Tables 1, 2, and Appendix 1). These results indicate that most pairs of Roseate Terns at these colonies are able to raise one chick relatively easily, but that only a variable proportion of them is able to raise a second chick. Predation is rare or absent in these colonies and most chicks that die fail to grow normally from hatching onwards (Nisbet 1978, 1981, Nisbet et al. 1990). Hence, the survival of B-chicks is probably limited by the rate at which the parents can feed the B-chick. This study shows further that survival of B-chicks from hatching to fledging is correlated across colonies and years with the growth of the survivors (Fig. 2). This suggests that differences between colonies and years in survival of B-chicks and, hence, overall productivity, reflect common factors that affect all parents. At least at BI, breeding adults utilize com-

TABLE 5. Results of analysis of covariance (ANOCOVA) for egg mass.¹

Independent variable	Regression coefficient	F	P
Location	- ²	24.35	<0.0001
Hatch date (A-chicks)	-0.0204 ³	15.05	<0.0001
Hatch order	- ²	14.45	0.0002
Year	- ²	3.12	0.025
Year × location	- ²	8.09	0.0003

¹ Based on all eggs ($n = 1,268$), including those that gave rise to chicks that did not survive to fledging (see text).

² Significant interactions with other variables.

³ Regression coefficient on hatch date for B-chicks was +0.0028 (not significant). Regression coefficients were not significantly different among all values of year and location. Regression coefficients for A- and B-chicks were significantly different from each other ($F = 7.58$, $P = 0.0005$).

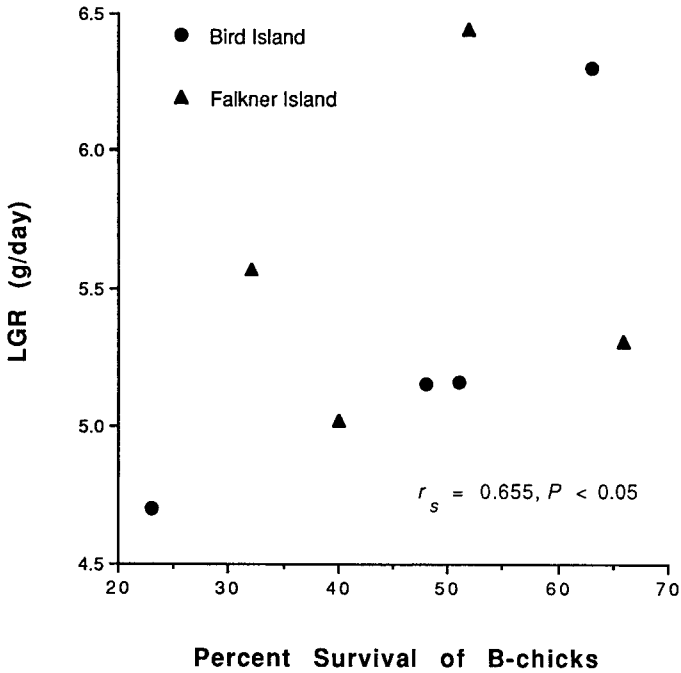


FIGURE 2. Relationship between average survival of B-chicks and average linear growth rate (LGR) in the survivors. Each point represents the mean values for one colony in one year: circles, Bird Island; triangles, Falkner Island.

mon feeding areas where they feed in loose aggregations (Nisbet 1981, D. Heinemann, pers. comm.), so that they have equal opportunities to catch prey. Hence, it is likely that differences in growth and survival of the B-chicks within a colony and year primarily reflect differences in parental quality, whereas differences between colonies and among years (Fig. 2) primarily reflect differences in average food availability or other environmental factors.

In addition to the strong dependence on hatch order, the results in this paper show significant dependence of both growth parameters on hatch date and egg mass (Tables 3 and 4). The relationships to egg mass may reflect correlations in mensural characteristics (larger females lay larger eggs, which give rise to larger chicks). The independent relationships to hatch date probably result from differences in parental performance (higher quality parents nest earlier) and/or seasonal declines in availability of prey. Older parents lay earlier and raise more young than do younger parents (Nisbet 1993, Burger et al. in press), so it is likely that at least some of the latter relationship results from differences in age or experience of the parents (cf. Furness 1983,

Pugesek 1993). Parental ages are known for only a fraction of our study chicks, however, and analysis of the effects of parental age will be deferred until a larger sample is obtained.

Nisbet (1978) earlier reported a correlation between LGR and egg mass among Roseate Terns at BI. This correlation persisted even when eggs were exchanged between parents that had laid small and large eggs. At first sight, this might appear to conflict with the hypothesis that LGR is dependent on characteristics of the parents. However, egg mass itself is determined by characteristics of the parents. In conjunction with the results reported in this paper, Nisbet's (1978) results suggest that differences in parental performance may be especially important in the period prior to egg-laying, and that the correlation between egg mass and subsequent chick growth and survival may be determined at that time.

Earlier studies at BI have shown a strong negative relationship between egg mass and laying date (Nisbet and Cohen 1975, Nisbet 1981, 1993). The results in this paper confirm this relationship (for A-eggs only) when all eggs are considered (Table 5), but not when analysis is limited to the eggs that gave rise to fledged chicks. The differ-

ence probably arises because chick survival is positively associated with egg mass and negatively associated with hatch date (Nisbet 1978, 1981, 1993, Burger et al. in press).

After controlling for effects of other variables, our results show few consistent differences between locations or among years. The most consistent difference was that 1989 was a good year for both survival and growth at BI, but a poor year at FI (Tables 1 and 2). Average productivity has been consistently lower at FI than at BI, not only in the four years of this study but in earlier and later years as well (authors' unpubl. data). Except for the difference in 1989 that was pointed out above, however, this difference resulted primarily from differences in average laying date, average clutch size, and hatching success, and was not manifested by consistent differences in chick survival or in average growth parameters (Fig. 2). Within the scope of this study, therefore, comparison of average growth parameters among colonies and years did not provide very useful information about differences in average environmental conditions. The differences that we found were small and inconsistent, and could have been detected by the simpler and less intrusive method of measuring average productivity (Nisbet et al. 1990). On the other hand, our results, like those of Furness (1983), suggest that individual growth parameters of chicks are useful indices of parental performance. They provide more information about individual differences in parental performance than is provided by the simple measure of success or failure in raising chicks. We plan to use these indices in future studies of individual parental performance and parental quality.

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APPENDIX 1. Mean masses (g) of A- and B-chicks according to age.

Age (days)	A-chicks			B-chicks		
	Mean	SD	n	Mean	SD	n
0	15.42	1.75	740	14.23	1.49	222
1	18.79	2.72	697	16.20	2.47	192
2	23.90	3.93	696	19.26	3.95	193
3	29.59	5.22	647	23.17	5.28	167
4	36.45	5.60	624	27.82	6.68	179
5	43.20	6.49	597	33.26	8.03	160
6	50.01	7.59	563	38.63	9.30	150
7	56.68	7.31	521	44.88	9.81	146
8	63.65	7.93	489	50.94	10.42	139
9	68.93	8.09	475	56.45	12.05	139
10	75.14	8.77	446	62.05	11.91	133
11	79.52	8.50	434	67.92	11.53	137
12	84.21	8.97	437	72.19	12.50	130
13	87.91	8.46	394	78.03	12.43	136
14	91.63	8.05	416	80.76	13.27	126
15	93.87	8.15	376	84.90	11.79	114
16	96.28	8.12	395	87.22	13.17	114
17	97.93	8.36	380	90.93	11.45	109
18	99.28	8.40	368	92.02	12.34	109
19	100.17	8.47	336	92.97	12.49	111
20	100.91	7.92	357	94.81	10.74	105
21	101.04	7.86	331	94.69	11.16	86
22	100.34	6.73	332	97.23	9.56	96
23	99.82	6.64	286	96.42	10.83	94
24	100.00	6.24	259	96.87	9.63	87
25	98.47	7.01	231	96.28	8.29	92
26	97.86	6.46	140	95.45	8.98	59
27	95.74	6.87	70	94.47	8.00	57
28	97.97	7.63	33	91.53	8.83	36
29	92.18	8.64	17	92.60	12.34	26
30	91.21	4.10	7	92.31	10.60	16