

VARIATIONS IN GROWTH OF ROSEATE TERN CHICKS: II. EARLY GROWTH AS AN INDEX OF PARENTAL QUALITY¹

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Abstract. We measured growth of Roseate Tern (*Sterna dougallii*) chicks at a colony in Connecticut in 10 successive years, 1987–1996. Data on body mass during the first 3–4 days of life were fitted to a quadratic regression model, yielding three parameters of early growth for each of 1,551 chicks: mass at hatching, linear growth, and quadratic growth. First chicks in each brood (A-chicks) exceeded second chicks (B-chicks) in each of the three growth parameters; A-chicks from broods of two grew faster during the first 3 days than single chicks. The three parameters of early growth depended upon egg mass, hatch order, hatch date, and year, but not on parental age after controlling for effects of the other variables. The linear and quadratic growth parameters were negatively correlated. Subsequent growth and survival of chicks were predicted by all three parameters of early growth. After controlling for effects of early growth, none of the other variables measured (hatch date, egg mass, parental age, hatching asynchrony, female–female pairing, or trapping) contributed significantly to explaining later growth or survival. Year effects were substantial in only 2 of the 10 years of study. Individual pairs were consistent in performance (as indexed by early growth) in successive years. These results suggest that growth and survival of Roseate Tern chicks are determined primarily by parental quality; much of the information about parental quality is expressed by the time the eggs are laid, and most of it is expressed by the time the chicks are three days old.

Key words: *age, Falkner Island, growth, parental quality, Roseate Tern, Sterna dougallii, variability.*

INTRODUCTION

Most studies of growth in bird chicks involve either fitting data to nonlinear sigmoid curves (Ricklefs 1968, Langham 1983, Brisbin et al. 1987), or deriving parameters from the middle or late stages of growth (Coulson and Thomas 1985, Lequette and Weimerskirch 1990, Nisbet et al. 1995). Such studies are necessarily limited to data from chicks that survive until late in the growth period, and in practice are largely limited to chicks that survive to fledging. However, investigation of the relationship between growth and survival requires data from chicks that do not survive. Because chick mortality in many species is concentrated in the early part of the

growth period, this requires data from the first few days of life. Few, if any, published studies of growth have focused specifically on this early period.

The first few days of life are an important period of growth for biological reasons also. At this time, parents must make the behavioral transition from incubation to feeding chicks. In many bird species, one parent is required to brood and guard newly-hatched chicks for much of the time, so that foraging time is limited even in species with biparental care. In most species, small chicks require very small food items and/or have special nutritional needs. In precocial or semi-precocial species, the chicks must learn to take and handle food. In species with asynchronous hatching, the first few days after hatching are the period when size differences are established, with important consequences for sibling

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competition and brood reduction. All these factors are known to be important in terns (*Sterna* spp., Gochfeld 1980, Wiggins and Morris 1987, Bollinger et al. 1990).

In this paper, we report a study of early growth in the endangered Roseate Tern (*S. dougallii*). We extend an earlier study (Nisbet et al. 1995) by analyzing data on the growth of Roseate Tern chicks during the first 3–4 days of life. We fit daily body-mass data from this period to a quadratic regression model, and use the three parameters derived from the model as measures of the early growth of each individual chick. We examine variations in these parameters in relation to year, egg mass, hatch date, brood size, hatch order, hatching asynchrony, parental age, female-female pairing, and trapping. We use 10 years of data from one of the two colony-sites included in the study by Nisbet et al. (1995). Data from the other site were available for 4 of the 10 years, but are not used in this paper because missing data from one or both sites precluded detailed comparisons.

Two principal questions addressed in the analysis are: (1) What factors are associated with variations in early growth? (2) To what extent do early growth parameters predict subsequent growth and survival? A third question addressed is the extent to which early growth of chicks reflects the “quality” of the parents. In several seabird species, there is evidence that variation in parental “quality” (Coulson 1968) contributes significantly to variation in performance (Coulson and Thomas 1985, Mills 1989, Bollinger 1994). Although parental “quality” is difficult to define independently of the outcomes that are measured, we use two approaches in this paper to avoid circularity. First, we examine the extent to which the performance of individual pairs is consistent among years, by comparing within-pair variance in growth parameters with total variance (for an earlier example of this approach, see Coulson and Thomas 1985). Second, we examine the extent to which growth parameters are predicted by parental characteristics which have been identified as indicators of “quality” in other studies, including laying date and egg-size. We also examine the extent to which growth parameters depend upon parental age, although improvement in performance with age is not usually considered to indicate an increase in phenotypic “quality” (Nisbet and Nager, in press).

METHODS

FIELD PROCEDURES

We studied Roseate Terns at Falkner Island, Connecticut (41°13'N, 72°39'W), a unit of the Stewart B. McKinney National Wildlife Refuge. This colony-site was described by Spendelov (1982). During the study period (1987–1996), Falkner Island supported between 130 and 190 pairs of Roseate Terns. Most pairs nested in artificial sites (nest-boxes or half-buried automobile tires). After hatching, chicks remained near the nests for variable periods before moving to natural hiding-places, mostly under rocks.

Study methods were described in detail by Nisbet et al. (1995). Almost all (95–100%) of the nests in the colony were studied in each year, although not all produced chicks. Study nests and eggs were marked when first found, usually at the time of laying. Except in 1987, about 95% of the eggs were weighed, usually on the day of laying. Nests were visited daily at the time of hatching; chicks were banded at hatching and were weighed on most days (always in the late afternoon) until they died, disappeared, or fledged. Most chicks that survived could be followed until they fledged. Most parents were color-banded with unique color-combinations (Spendelov et al. 1994). From banding of chicks since 1977, many parents were of known age; the proportion of known-aged birds increased from 39% in 1987 to 68% in 1996. Sexes were determined by observation of copulation and/or by persistent courtship-feeding; a few pairs of birds attending clutches of 3–5 eggs, or clutches of two eggs with laying intervals ≤ 1 day, were identified as female-female pairs (Nisbet and Hatch, in press). The proportion of known-sex birds increased from 31% in 1987 to 86% in 1996.

TERMINOLOGY

Variables used in the statistical analysis are defined as follows. Hatch order: *A1*, only chick in brood of 1; *A2*, first chick in brood of 2 or more; *A*, either *A1* or *A2*; *B*, second chick in brood of 2 or more. Although a few third chicks hatched, only one survived more than 5 days (Spendelov et al. 1997a); this chick is not included in the analysis. Hatch date is the date of hatching of each chick (1 May = 1). The day of hatching for each chick is designated day 0. Age difference is the age in days of the *A*-chick on the day

the *B*-chick hatched (mean 2.63 days, range 0–8 days). Mass difference is the difference (in g) between the masses of the *A*- and *B*-chicks on the day the *B*-chick hatched (mean 16.3 g, range 1.7–36.5 g). Male age and female age are the ages in years of the male and female parents, where known from banding as chicks. Pair age is the age of the parent whose age was known, or the average age in cases where both parents were of known age. FF-pair takes the value 1 if both parents were sexed as female (5.0% of cases), 0 otherwise. Trapped takes the value 1 if one or both parents were trapped during the nesting cycle (65.4% of cases), 0 otherwise.

STATISTICAL PROCEDURES

Statistical analyses were conducted using SAS (1995). Mass data for days 0–3 (*A*-chicks) or days 0–4 (*B*-chicks) were fitted to a quadratic regression model:

$$M_d = M_0 + ad + bd^2, \quad (1)$$

where M_d = chick mass on day d , M_0 = estimated chick mass on day 0, d = age in days, a = linear growth parameter, and b = quadratic growth parameter. a is the instantaneous slope (tangent) of the growth curve on day 0. b is a measure of the curvature of the growth curve: the mass of the chick is estimated as ($M_0 + 3a + 9b$) on day 3 and ($M_0 + 4a + 16b$) on day 4

(see Fig. 1). M_0 , a , and b were estimated for each chick for which mass was measured on day 0 and at least two other days, using the general linear models procedure of SAS.

Two parameters were calculated to characterize growth of chicks after age 3–4 days. Linear growth rate (LGR) is defined as the slope of a regression line fitted to mass data during the quasi-linear period of growth (3–12 days for *A*-chicks, 4–13 days for *B*-chicks). LGR was calculated only for chicks with at least 4 data points within this period. Asymptotic mass (AM) is defined as the mean of all masses (minimum of two) measured during the period of near-constant mass (17–28 days for *A*-chicks, 18–29 days for *B*-chicks). These parameters are the same as those used by Nisbet et al. (1995), except that LGR is defined for periods of growth one day shorter than in the earlier paper.

Analysis of variance (ANOVA) was used to analyze the dependence of M_0 , a , and b on categorical variables (year, brood size, hatch order, and their interactions). 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 homogeneity of variances of the residuals.

Analysis of covariance (ANOCOVA) was used to analyze the simultaneous effects of cat-

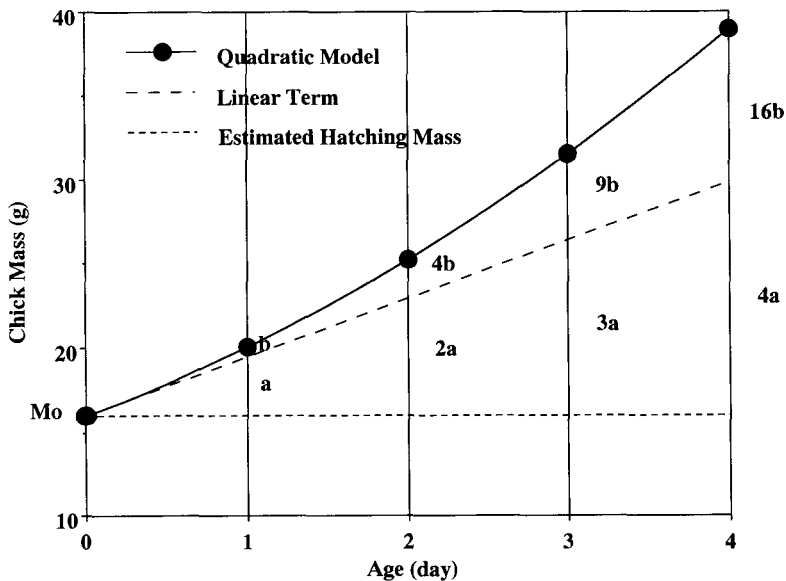


FIGURE 1. Quadratic regression model used for fitting to early growth data of Roseate Tern chicks.

egorical and continuous variables (hatch date, egg mass, parental age, age difference, and mass difference) on M_0 , a , and b . The general linear model was as follows:

$$\begin{aligned} \gamma_{ij} = & C_{ij} + H_{ij}(\text{hatch date}) \\ & + E_{ij}(\text{egg mass}) + P_{ij}(\text{parental age}) \quad (2) \\ & + A_{ij}(\text{age difference}) \\ & + M_{ij}(\text{mass difference}) + \text{error}, \end{aligned}$$

where i and j index hatch order and year, respectively, γ_{ij} is the dependent variable (M_0 , a , or b), C_{ij} is an intercept term, and H_{ij} , E_{ij} , P_{ij} , A_{ij} , and M_{ij} are regression coefficients. ANOCOVA compares these regression coefficients among the categorical variables i and j . Initially, the model was used to estimate slopes and intercepts separately for each of the 27 combinations of i and j . Reduced models (constraining parameters over various combinations of the categorical variables) were then explored until the most parsimonious model consistent with the data was found. The criterion for rejection of a reduced model was $P < 0.005$ for the likelihood ratio F -test comparing the constrained parameters of the reduced versus the full model. The probability level of 0.005 was selected for this criterion because the large sample sizes meant that very small effects could be "significant" at $P < 0.05$. Within the models selected as most parsimonious, the contributions of independent variables were evaluated using likelihood ratio F -tests, with a criterion for significance of $P < 0.05$. In all analyses testing the effects of parental age, we ran separate models using the variables male age, female age, and pair age; the age of both parents was known in only 23% of cases, so the sample sizes were too small to test the effects of male and female age simultaneously. In some analyses, FF-pair and trapped were included as additional categorical variables.

Logistic analysis of covariance (LANOCO-VA) was performed using the CATMOD procedure of SAS (1995) to analyze the dependence of chick survival on categorical and continuous variables. This analysis was performed separately for A - and B -chicks, because A -chicks survived much better than B -chicks (93.5% vs 42.0%), and it was expected that the dependence of survival on growth parameters would be much stronger for B -chicks. The model used was:

$$\begin{aligned} \ln(p_i/1 - p_i) = & C_i + H_i(\text{hatch date}) \\ & + E_i(\text{egg mass}) \\ & + P_i(\text{parental age}) \\ & + A_i(\text{age difference}) \\ & + M_i(\text{mass difference}) \\ & + \text{error}, \quad (3) \end{aligned}$$

where p_i is the probability of survival and i indexes year. Conceptually, LANOCOVA bears the same relationship to multiple logistic regression as ANOCOVA does to multiple linear regression. Except for the change in the dependent variable, analytical procedures were similar to those used in the ANOCOVA. LANOCOVA models were compared using likelihood ratio χ^2 -tests rather than F -tests, however, and Wald χ^2 -tests (SAS 1995) were used to test the significance of individual variables in the final models selected.

For all the above analyses, all nestings were treated as independent events, even though many parents nested at Falkner Island in several different years. To compare within-pair variability with overall variability, we calculated the standard deviation (SD) of each growth parameter for each pair in which both individuals nested together in more than one year (re nesting pair), performing separate analyses for A - and B -chicks. On average, re nesting pairs nested together for about 2.5 years ($SD = 1.2$) during the 10-year study. We then calculated the mean SD (and its standard error, SE) for each parameter over all re nesting pairs. We also calculated the overall SD of each parameter over all pairs; re nesters were included in this calculation because we wanted to compare re nesting pairs with all pairs, not just with non-re nesting pairs. To test for differences between within-pair and overall variability, we performed two-tailed Z -tests, using the SE of the mean SD among all pairs to estimate the variance of the distribution of the overall mean SD. Normality can be assumed for the mean SDs because of the large sample sizes ($n > 50$).

Correlations between growth parameters (among hatch orders or years) were assessed using Pearson or Spearman rank correlation coefficients.

RESULTS

PATTERNS OF EARLY GROWTH

We studied 601 broods of two chicks and 401 broods of one chick; mean brood-size was 1.60.

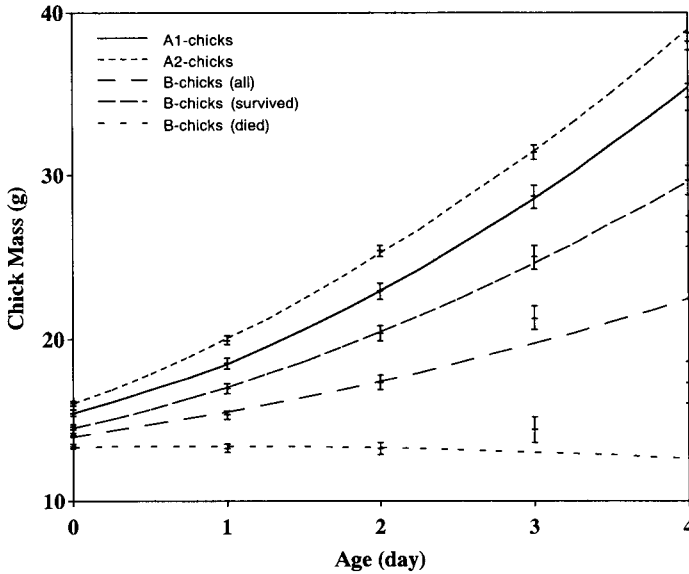


FIGURE 2. Growth of Roseate Tern chicks during the first four days of life, classified by hatch order and (for *B*-chicks) survival. Sample sizes are shown in Table 1. The lines show the regression models obtained by averaging the model parameters over all chicks within each category. The horizontal bars show the means \pm 2 SE of all masses measured for chicks within each category on each day of life. On each day of life, mean masses of chicks in each of the five groups were significantly different from each other (Tukey's tests, $P < 0.001$ in all cases). For *B*-chicks that died and for all *B*-chicks, the measured means deviate from the regression models after day 2, because chicks that died early had lower masses on days 0–2 than chicks that survived to the age of 3–4 days.

Figure 2 summarizes the mean masses of chicks on each day of life, grouped by hatch order and (for *B*-chicks) survival. Table 1 presents summary statistics for the three growth parameters (M_0 , a , and b), grouped by hatch order but pooled over all years.

On average, *A2*-chicks had higher initial masses and grew faster than *A1*-chicks, which in turn had higher initial masses and grew faster than *B*-chicks (Fig. 2). All differences at each day of age were highly significant (Tukey's tests, $P < 0.001$ in each case). Mean masses of *A1*- and *A2*-chicks showed close fits to the quadratic regression model through day 3 (Fig. 2), but be-

gan to deviate on day 4 as the growth curve approached linearity (Nisbet et al. 1995). Mean masses of *B*-chicks that survived to fledging showed a close fit to the quadratic regression model through day 4, but mean masses of *B*-chicks that died deviated from the model after day 2 (Fig. 2). This deviation resulted from the fact that *B*-chicks with lower or negative growth rates started to die by day 2, so that the mean masses recorded on days 3–4 reflected above-average growth. The relationship between survival and growth is analyzed further below.

On average, even the *B*-chicks that survived to fledging had, by day 4, fallen about one day

TABLE 1. Mean (\pm SE) values of early growth parameters of Roseate Tern chicks, grouped by hatch order but averaged over all years.^a

Parameter	Hatch order		
	<i>A1</i>	<i>A2</i>	<i>B</i>
M_0	15.48 \pm 0.10B	16.03 \pm 0.08A	14.05 \pm 0.07C
a (g day ⁻¹)	2.47 \pm 0.13B	3.46 \pm 0.12A	1.29 \pm 0.11C
b (g day ⁻²)	0.63 \pm 0.05A	0.57 \pm 0.04A	0.21 \pm 0.03B
n	398	601	552

^a Entries in the same line that do not share the same letter are significantly different (Tukey's test, $P < 0.05$).

TABLE 2. Results of analyses of covariance (ANOCOVAs) for early growth parameters of Roseate Tern chicks.

Independent variable	Dependent variable		
	M_0	a	b
Continuous variables (regression coefficients)			
Egg mass	+0.722***	ns	ns
Hatch date	-0.039 g day ⁻¹ ***	-0.079 g day ⁻² ***	-0.031 g day ⁻³ ***
M_0	—	ns	+0.197 day ⁻² ***
a	—	—	-0.196 day ⁻¹ ***
Categorical variables			
Hatch order	***a	***a	*a
Year	***b	***b	ns
Interactions			
$a \times$ Hatch order	—	—	***c
$M_0 \times$ Hatch order	—	ns	*c
$M_0 \times$ Year	—	ns	*c
Model			
R^2	0.49	0.21	0.74
F	64.8***	16.2***	28.2***
df	13, 864	14, 863	81, 746

* $P < 0.05$; *** $P < 0.001$; ns, $P > 0.05$; —, not included in model.

^a Intercepts were higher for A-chicks than for B-chicks (by 1.03 g for M_0 , 1.83 g day⁻¹ for a , 2.25 g day⁻² for b); there was no significant difference between A1- and A2-chicks in each case.

^b Intercepts for M_0 were high in 1989, 1992, and 1994, and low in 1988 and 1991. Intercepts for a were high in 1992, 1993, and 1994, and low in 1990, 1991, and 1996.

^c See text for effects of interactions.

behind their older siblings in mass growth (Fig. 2); this was additional to the usual hatching interval of 2.5–3 days (mean \pm SD = 2.63 \pm 0.86 days within this data set).

DEPENDENCE OF EARLY GROWTH ON HATCH ORDER AND YEAR

ANOVA indicated that mass at hatching (M_0) depended upon both hatch order ($F_{2,1521} = 160$, $P < 0.001$) and year ($F_{9,1521} = 7.2$, $P < 0.001$), with no significant interactions (overall $R^2 = 0.22$). The linear growth parameter (a) similarly depended upon both hatch order ($F_{2,1521} = 97$, $P < 0.001$) and year ($F_{9,1521} = 9.6$, $P < 0.001$), with no significant interaction (overall $R^2 = 0.17$). Among years, M_0 and a were positively correlated ($r_s = 0.54$, $P < 0.01$, pooling data over all hatch orders), both being high in 1992, 1993, and 1994, and both being low in 1987, 1990, and 1996. The quadratic growth parameter (b) also depended upon both hatch order ($F_{2,1521} = 33$, $P < 0.001$) and year ($F_{9,1521} = 2.31$, $P = 0.014$), but with significant interaction ($F_{18,1521} = 2.19$, $P = 0.003$). Among years, a and b were inversely correlated ($r_s = -0.58$, $P < 0.01$, pooling data over all hatch orders). Differences in residual variance among years and hatch orders were generally small and are ignored in the anal-

ysis, although Bartlett's test indicated significant inhomogeneity of variances in all cases ($P < 0.01$) because of the large number of categories. However, logarithmic transformation did not help, so we rely on the robustness of ANOVA to departures from homogeneity (see Scheffé 1959). Because of the inequality of variances, significance levels reported subsequently for tests under ANOVA and ANOCOVA are only approximate.

DEPENDENCE OF GROWTH ON HATCH DATE, EGG MASS, AND PARENTAL AGE

Table 2 presents the results of ANOCOVAs for M_0 , a , and b . These analyses utilize data for only nine years, because egg masses were not measured in 1987. Initially, the analyses were run without the variables FF-pair, trapped, age difference, and mass difference. Mass at hatching (M_0) depended upon egg mass, hatch order, hatch date, and year ($P < 0.001$ in each case; Table 2), but not on parental age ($P > 0.1$ for male age, female age, and pair age). Interactions were not significant (overall $P = 0.04$). The linear growth parameter (a) depended upon hatch date, hatch order, and year ($P < 0.001$ in each case), but not egg mass, M_0 , or any parental age variable ($P > 0.1$ in each case; Table 2). Inter-

TABLE 3. Results of logistic analyses of covariance (LANOCOVARs) for survival of Roseate Tern chicks.^a

Independent variable	Hatch order	
	A-chicks	B-chicks
Continuous variables [regression coefficients (odds ratios)] ^b		
<i>a</i>	+0.65 g ⁻¹ day (1.9)***	+1.24 g ⁻¹ day (3.5)***
<i>b</i>	+1.95 g ⁻¹ day ² (7.0)***	+3.98 g ⁻¹ day ² (52.6)***
<i>M</i> ₀	ns	+0.42 g ⁻¹ (1.5)***
Categorical variable		
Year	*** ^c	*** ^c

*** $P < 0.001$; ns, $P > 0.05$ (Wald χ^2 -tests).

^a The models correctly classified 24.6% (16/65) of A-chicks that died, 99.5% (929/934) of A-chicks that survived, 86.6% (201/232) of B-chicks that died, and 89.1% (285/320) of B-chicks that survived.

^b See equation (3) for logistic model. Positive regression coefficients indicate positive relationships between survival and the independent variables in all cases.

^c The intercept for A-chicks was low in 1996 (-3.74, odds ratio = 0.097). The intercept for B-chicks was low in 1995 (-8.46, odds ratio = 0.163) and 1996 (-9.54, odds ratio = 0.055).

actions were marginally significant (overall $P = 0.01$), but contributed very little to the explained variance and are ignored in this analysis. The quadratic growth parameter (*b*) depended upon *a*, hatch date, and *M*₀ ($P < 0.001$ in each case; Table 2); the largest contribution to the model was a negative regression on *a* ($F_{1,796} = 1,436$). Hatch order entered the model through an interaction with *a*, such that the dependence of *b* on *a* was much stronger for A-chicks than B-chicks. Otherwise, interactions among independent variables were not significant at the $\alpha = 0.005$ level used for fitting the model. Year appeared in the model only through a weak interaction with *M*₀ (Table 2). After controlling for these variables, there was no dependence of *b* on egg mass ($P > 0.05$) or any parental age variable ($P > 0.5$).

Inclusion of the variables FF-pair and trapped made no significant contributions to the explained variances of *M*₀ or *a*. For *b*, the improvement was highly significant ($P < 0.001$), but R^2 increased only from 0.742 to 0.755. The only significant term in these variables that entered the model was the interaction *M*₀ × trapped: the regression coefficient of *b* on *M*₀ was reduced by 0.078 day⁻² for chicks whose parent(s) had been trapped. Inclusion of the variables age difference and mass difference made no significant contribution to the explained variance or to individual terms in the model.

DEPENDENCE OF CHICK SURVIVAL ON EARLY GROWTH

Table 3 summarizes the results of LANOCOVAR on survival data for Roseate Tern A- and B-chicks at Falkner Island, 1987–1996. In the first analyses, survival was related to parameters of

early growth (*M*₀, *a*, and *b*), year, and (for B-chicks only) age difference and mass difference. The most parsimonious models had the same slopes (dependence on *M*₀, *a*, and *b*) for all years, but different values of the intercept for different years. Survival of both A- and B-chicks was significantly positively related to *a* and *b* ($P < 0.001$ in all cases), and to year, being low in 1996 ($P < 0.001$) and 1995 ($P < 0.001$ for B-chicks only) after controlling for *M*₀, *a*, and *b*. Survival of B-chicks also was positively related to *M*₀ ($P < 0.001$), but the relationship of survival of A-chicks to *M*₀ was not significant ($P = 0.08$). Age difference and mass difference did not contribute significantly to explaining the survival of B-chicks ($P > 0.1$ in each case). Likewise, inclusion of egg mass, FF-pair, and any parental age variable did not contribute significantly to the explained variance ($P > 0.1$ in all cases). Inclusion of hatch date, however, led to significant increases in the explained variance ($P < 0.005$, odds ratio = 0.911, for A-chicks; $P < 0.05$, odds ratio = 0.886, for B-chicks). Inclusion of the variable trapped led to a marginally significant increase in the explained variance for B-chicks only ($P = 0.05$, odds ratio = 2.67), but the relationship was positive (higher survival of B-chicks from parents that had been trapped).

We next used LANOCOVAR to examine the dependence of the survival of B-chicks on laying variables only. Survival was significantly related to hatch date ($H_i = -0.072$ day⁻¹, $P < 0.001$, odds ratio = 0.931, for A-chicks; $H_i = -0.060$ day⁻¹, $P < 0.001$, odds ratio = 0.942, for B-chicks) and egg mass ($E_i = +0.28$ g⁻¹, $P < 0.001$, odds ratio = 1.32, for B-chicks; ns for A-chicks). However,

TABLE 4. Results of analyses of covariance (ANOCOVAs) for linear growth rate and asymptotic mass.

Independent variable	Dependent variable	
	Linear growth rate (LGR)	Asymptotic mass (AM)
Continuous variables (regression coefficients)		
M_0	ns	-0.070*
a	+0.384***	+2.93 day***
b	+1.27 day***	+9.28 day ² ***
Categorical variables		
Hatch order	***a	***a
Year	ns	ns
Interactions		
$a \times$ Hatch order	***b	**b
$b \times$ Hatch order	***b	**b
$a \times$ Year	***c	**c
$b \times$ Year	ns	**c
$M_0 \times$ Hatch order	ns	*d
$M_0 \times$ Year	ns	**e
Model		
R^2	0.27	0.34
F	7.2***	8.6***
df	65, 1246	65, 1079

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns, $P > 0.05$.

^a Intercepts were higher for A2-chicks than for B-chicks (by 2.74 g day⁻¹ for LGR, 13.4 g for AM); there was no significant difference between A1- and B-chicks in either case.

^b The regression coefficients on a and b tabulated are those for B-chicks. The regression coefficients for A-chicks were significantly smaller in each case (no differences between A1- and A2-chicks).

^c The regression coefficients on a and b tabulated are those for 1996. Regression coefficients were significantly smaller in 1994, but not in other years.

^d The regression coefficient on M_0 tabulated is that for B-chicks. The regression coefficient for A2-chicks was -0.480 (significantly different from that for B-chicks, $P < 0.01$); that for A1-chicks was -0.023 (not significantly different from that for B-chicks).

^e The regression coefficient on M_0 tabulated is that for 1996. The only year for which the regression coefficient was significantly different ($P < 0.05$) was 1992 (regression coefficient = 1.01).

the proportions of chicks correctly classified were smaller than those from the models reported in Table 3: 0% (0/55) of A-chicks that died, 100% (837/837) of A-chicks that survived, 33.3% (70/210) of B-chicks that died, and 79.9% (226/283) of B-chicks that survived.

DEPENDENCE OF LATER GROWTH AND ASYMPTOTIC MASS ON EARLY GROWTH

Results of ANOCOVAs indicate that both linear growth rate (LGR) and asymptotic mass (AM) depended upon a , b , and hatch order; interactions between these variables were significant, such that the dependence of both LGR and AM on a and b was much greater for B-chicks than for A-chicks (Table 4). After controlling for these variables, the only effect of M_0 was a small contribution to the explained variance of AM (largely limited to A2-chicks and to 1992). Year appeared only through interactions with other variables, with 1994 standing out as the only year in which later growth did not depend significantly on earlier growth.

CONSISTENCY IN PERFORMANCE OF PAIRS AMONG YEARS

Table 5 compares the variability of growth parameters within pairs that were studied in two or more years with that among all pairs. In all cases, within-pair variance was significantly lower than overall variance ($P < 0.001$ for 8/10 comparisons; $P < 0.05$ for 2/10 comparisons).

WITHIN-BROOD CORRELATIONS

Correlations between the growth parameters of siblings were generally small; only 4/9 of the correlation coefficients were significantly different from zero (Table 6). Early growth parameters of B-chicks were correlated with mass at hatching and a of their older siblings, but not with b of their older siblings.

DISCUSSION

Because early growth of bird chicks is usually nonlinear, several data points are required to characterize this part of the growth curve. Except for B-chicks that died early, our data for

TABLE 5. Comparison of within-pair with overall variability in early growth parameters.

Parameter compared	Estimate of variability		P-value ^a
	Within-pairs (Mean SD \pm SE, n)	Overall (SD, n)	
A-chicks			
M_0	1.36 \pm 0.08 (147)	2.04 (999)	<0.001
<i>a</i>	2.01 \pm 0.10 (147)	2.84 (999)	<0.001
<i>b</i>	0.72 \pm 0.04 (147)	0.98 (999)	<0.001
LGR	0.74 \pm 0.05 (165)	1.09 (1,052)	<0.001
AM	4.01 \pm 0.24 (148)	6.90 (935)	<0.001
B-chicks			
M_0	1.00 \pm 0.08 (81)	1.64 (552)	<0.001
<i>a</i>	2.18 \pm 0.16 (81)	2.66 (552)	<0.001
<i>b</i>	0.65 \pm 0.05 (81)	0.76 (552)	<0.03
LGR	1.04 \pm 0.13 (55)	1.73 (357)	<0.001
AM	7.69 \pm 1.04 (50)	10.43 (310)	<0.01

^a Two-tailed Z-tests.

Roseate Terns fit closely to the quadratic regression model (Fig. 2), so that three data points (for days 0, 1, and 2) are sufficient to characterize early growth in this species. Only 3.2% of the chicks included in this study (3/1,002 A-chicks and 49/601 B-chicks) died or disappeared before the age of 2 days (most chicks that died did so between days 2 and 7). Hence, our data should not have been biased significantly by the loss of these chicks that dropped out of the study before we could determine growth parameters for them.

A noteworthy feature of our results is that the linear and quadratic growth parameters (*a* and *b* in our notation) were inversely correlated with each other, both among individual chicks and among years. In other words, when initial growth was slow, this was compensated for by more accelerated growth over the next few days. This suggests that growth was partly regulated, the mass at age 3 days being less variable than would have been predicted if variations in *a* and *b* had been independent.

Among Roseate Terns at Falkner Island, most A-chicks survived to fledging in each year, so that the productivity of the parents was determined primarily by the survival of B-chicks (Nisbet et al. 1995). Survival of B-chicks was predicted very well by early growth parameters; within years, more than 87% of B-chicks could be classified correctly by data from the first three days of growth alone (Table 3). Later growth and asymptotic mass (i.e., condition at fledging) of the B-chicks that survived to fledging also were predicted reasonably well by early growth

parameters (Table 4). Survival, later growth, and asymptotic mass of A-chicks also were related to early growth parameters in the same ways, but the relationships were much less strong than for B-chicks (Tables 3 and 4). Classification of A-chicks that died based upon early growth parameters was especially poor (see footnote a to Table 3).

The consistency in performance of pairs that bred together in more than one year (Table 5) indicates that breeding performance is determined primarily by parental "quality" (cf. Coulson and Thomas 1985). Nevertheless, after controlling for early growth parameters, neither parental age nor the factors that we used as indices of parental quality (hatch date and egg mass) contributed significantly to the explained variance of either later growth or survival of Roseate Tern chicks, except for a small effect of hatch date on survival (Tables 3 and 4). This suggests that parental quality is fully expressed by the parental characteristics that determine chick growth during the first few days of life. Although parental performance undoubtedly contributes to growth and survival of chicks after the first few days, our data suggest that this later performance must be highly correlated with early performance.

Early growth parameters were themselves predicted fairly well by laying date and egg mass, i.e., characters that were manifested at the time of egg-laying. Again, parental age (whether indexed as male age, female age, or pair age) did not enter the models as an additional predictive variable (Table 2). This suggests that parental quality was already fairly well expressed by the time the eggs were laid, in the sense that high quality birds laid early and laid large eggs, regardless of age. However, chick survival was not so well predicted by these egg characters alone; prediction was especially poor for chicks that died (0% correct classification for A-chicks, 33% for B-chicks). This contrasts with 89% correct classification of B-chicks that died, using early growth parameters and year variables only (Table 3). Poor survival of chicks in 1995 and 1996 (see below) explains part of this difference, but the large magnitude of the difference suggests that B-chicks from early and/or large eggs survived poorly at this site in other years also.

We investigated several other variables (FF-pair, trapped, age difference, and mass difference), but found that they did not contribute sig-

TABLE 6. Within-brood correlations between early growth parameters of A- and B-chicks.^a

B-chicks	A-chicks		
	M_0	a	b
M_0	+0.247***	+0.107*	-0.035
a	+0.020	+0.095*	+0.004
b	+0.130**	-0.022	+0.050

^a All values tabulated are Pearson correlation coefficients ($n = 480$). * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; other entries, $P > 0.05$; P -values are not adjusted for multiple comparisons.

nificantly to the statistical predictions of growth and survival. About 5% of the chicks included in this study were attended by female-female pairs. On average, female-female pairs raise fewer young than female-male pairs, mainly because of low fertilization rates (Nisbet and Hatch, in press). We initially hypothesized that chicks of female-female pairs might also grow more slowly than those of female-male pairs, because the primary role in early chick-feeding by Roseate Terns is taken by the male (Wagner and Safina 1989, D. Shealer, unpubl. data). Likewise, we hypothesized that chicks might grow more slowly if their parents had been trapped, because trapped birds are sometimes slow to return to the nest and resume parental care (Nisbet 1981, Burger et al. 1995). Because the variables age difference and mass difference reflect the disparity in size between A- and B-chicks, and because differences in size are thought to intensify competition for food between siblings in other species (Bollinger et al. 1990, Sydeman and Emslie 1992), we hypothesized that these variables also might be correlated negatively with growth and survival of B-chicks. However, the statistical analyses reported in this paper provided no support for any of these hypotheses (except for a small effect of trapping, which will be examined in detail in a later study). The fact that the early growth of the B-chicks was predicted by variables established at the time of egg-laying, despite wide variation in the degree of hatching asynchrony, indicates that parental quality was more important than sibling competition in determining chick growth. Pugesek (1983) reached a similar conclusion for California Gulls (*Larus californicus*), using a different method of analysis. Although sibling competition may in fact be more important in other species than in Roseate Terns, we suggest that more rigorous multivariate analysis is needed to demonstrate this.

Chick growth and survival are influenced not

only by factors intrinsic to the parents, but also by extrinsic factors such as predation, weather, and food availability. This study was continued for 10 years with the expectation that variability in these extrinsic factors would be reflected in year-to-year variability in growth and survival. In fact, although early chick growth varied significantly from year to year, much of this variability disappeared after controlling for egg variables (Table 2). Similarly, year effects made relatively small contributions to the explained variance of later growth parameters and chick survival (Tables 3 and 4). After controlling for other variables, all year effects were nonsignificant or small, except those listed in footnote c to Table 3: low survival of B-chicks in 1995 and very low survival of both A- and B-chicks in 1996. 1996 was noteworthy at Falkner Island as a year with heavy predation on chicks by Black-crowned Night-Herons (*Nycticorax nycticorax*); this was the only year with substantial predation during the 10-year study (Zingo et al. 1997). In 1995, many B-chicks which had grown well during the first few days later grew very slowly and many died from starvation at ages 15–30 days; this is thought to have resulted from a decline in food availability late in the season (Spenderlow et al. 1997b).

In summary, chick growth and chick survival in Roseate Terns appear to be determined primarily by aspects of parental performance that are consistent within individual pairs and hence meet the definition of parental "quality." These aspects of parental quality are already manifested at the time of egg-laying and are almost fully expressed by chick growth during the first few days of life. In most years, later growth and chick survival were very well predicted by measures of early growth. After controlling for variations in laying date, egg mass, and early growth parameters, breeding performance was very consistent from year to year (1987–1994): substantial year effects were not detected until the last two years (1995–1996) of the 10-year study.

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