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# Food Addition and Twinning Experiments in the Cape Gannet: Effects on Breeding Success and Chick Growth and Behavior

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**Abstract.**—Breeding success and growth of single and twinned Cape Gannet (*Morus capensis*) chicks under natural and supplementary food regimes were studied at Malgas Island, Saldanha Bay, South Africa. Age differences between chicks in artificially twinned broods were set at 0, 5, and 10 days in 1986-87, and 0 and 5 days in 1987-88. The additional food supplied was ca 5% of the body mass (25% of chicks daily food intake). The number of fledglings per nest (singletons and twins pooled) by controls ( $0.72 \pm 0.07$  (S.E.),  $N = 85$ ) and food supplemented birds ( $0.78 \pm 0.07$ ,  $N = 78$ ) did not differ significantly. A total of 159 (out of 273) chicks died, of which 75% died by starvation. Mortality was high during the first 20 days and decreased significantly with age. No significant differences in mortality rate were observed between control and food supplemented chicks. Masses of twinned chicks did not differ from masses of singletons. The growth parameters of fledging mass, length of fledging period, and age at maximum body mass did not differ significantly between control chicks and those provided with extra food. Brood-type effect was significant only on maximum body mass attained by chicks. Chick begging frequency was higher in  $0_{-5}$ twins than in  $0_{-0}$ twins or singletons, however, the number of parental feeds per chick was similar in all brood types. Success rate (the percentage of begging bouts that resulted in parental feeding) was significantly higher in  $0_{-0}$ twins and singletons than in  $0_{-5}$ twins. Success rate, begging frequency and priority ratio (the probability that one chick obtained food first when both chicks begged simultaneously) were similar between *a*- and *b*-chicks in twins. The results suggest that chicks regulate their food intake and cannot increase their growth rate in response to the extra food. The mechanism for this is probably a behavioral feed-back link to adult provisioning rate. The study does not support the hypothesis of Cape Gannet numbers being limited by food during the breeding season (Ashmole's hypothesis), suggesting instead high food availability during the study period. Received 26 June 1990, accepted 25 March 1991.

**Key words.**—Ashmole's hypothesis, breeding success, twinning experiments, food addition, Cape Gannet, *Morus capensis*, South Africa.

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In seabirds, population regulation is thought to be density-dependent, and mediated by food shortage. Two contrasting hypotheses based on a density-dependent control mechanism have been proposed. Ashmole (1963) proposes that food shortage during the breeding season (depletion of resources around the colony leading to increased competition for food) can reduce the reproductive output of the population, and hence regulate population size. Alternatively, Lack (1966) maintains that the principal mechanism regulating seabird numbers is density-dependent mortality (food mediated) of young birds outside the breeding season.

Assessments of the impact of food availability on breeding success of birds generally are based on indirect estimates of food availability (e.g. Blancher and Robertson 1987, Hussell and Quinney 1987). Breeding success and chick growth have been used to assess food availability to breeding birds, especially in seabirds

(e.g. Anderson *et al.* 1982, Corkhill 1973, Pettit *et al.* 1984, Ricklefs *et al.* 1984, 1985). Direct measurement of food availability is often difficult, because the resource cannot be sampled in a way that represents food availability to the animal in question. However, experimental manipulation of food availability to adults or chicks can overcome this problem. For example, additional food given to the chicks during the nestling period resulted in faster growth and higher fledging mass of puffins (*Fratercula arctica*; Harris 1978), but not of Tufted (*F. cirrhata*) and Horned (*F. corniculata*) Puffins (Wehle 1983).

Twinning experiments, in which parents are given additional chicks to rear, have been used to provide information on optimal brood size and effects of food limitation in gannets and other birds (Anderson 1976, Corkhill 1973, Harris 1970, Jarvis 1974, Nelson 1964). Nelson (1964) for example, found that pairs of North Atlantic Gannets (*Morus bassanus*) could success-

fully raise experimental twins to fledging in the absence of supplementary food. However, Jarvis (1974) in similar twinning experiments with the Cape Gannet (*M. capensis*), found that birds were less successful in raising twins: the average body mass of twins during the nestling period and at fledging was lower than that of single chicks. Thus, Jarvis's findings provide circumstantial evidence in support of Ashmole's hypothesis.

With regard to twinning and food supplementation experiments, Ashmole's hypothesis makes some testable predictions. Under conditions of food shortage, twins will have a poorer growth performance and a lower probability of fledging than singletons. In addition, food supplementation should increase the fledging success of both twins and singletons. To examine significance of food availability as a primary factor determining brood size and breeding success, and ultimately in regulating numbers, I evaluated the reproductive performance of Cape Gannets subject to differing food availability. In contrast to Jarvis's study, I created a gradient of food demand on adults, from reduced to doubled food demand, by a combination of brood size manipulation and supplying extra food to chicks.

Brood manipulation experiments in many seabirds is achieved by increasing the brood from one chick, the natural condition, to two (e.g. Nelson 1964, Jarvis 1974). However, the behavioral implications of the unnatural situation are often not carefully documented and their bearing on the experimental aims are not examined in detail. For an artificially enlarged clutch it is obviously important whether the eggs hatch synchronously or asynchronously, since this may influence hatching success and nestling survival (Slagsvold 1982). This essential factor has been overlooked in the twinning experiments made so far in seabirds. So, an additional objective of this paper was to examine to what extent chick behavior and parent-chick behavioral interactions in experimentally enlarged broods may influence the results of twinning experiments. Specifically, I attempt (1) to compare the reproductive success of synchronously and asynchronously hatched broods, and (2) to assess the chick-chick and chick-parent be-

havioral interactions in synchronously and asynchronously hatched broods. These comparisons will give some guidelines on the most suitable twinning experimental design.

## METHODS

### Study area and population

The study was conducted at Malgas Island (33°03'S, 17°55'E), in the Benguela upwelling system of the South African west coast (see Duffy and La Cock 1985 for a description of the island). The breeding population of Cape Gannets at Malgas Island in 1969 was estimated at 13 600 pairs increasing to nearly 20 200 pairs by 1980 (Crawford *et al.* 1983). In 1985 the Cape Gannets breeding at Malgas Island were estimated at 28 900 pairs (Berruti 1987).

### Experimental design

In 1986-87 newly hatched chicks or pipping eggs from elsewhere in the colony were used to replace the nest contents of 103 experimental nests, of which 74 were twinned. Age differences between twins were set at 0, 5, and 10 days (the notation 0-0, 0-5 and 0-10 refers to the age structure of the twins). As fledging mass of Cape Gannet chicks is related to hatching date (Jarvis 1974), the experiment was set up during the peak hatching period (second and third week of November) to control for this factor. Chicks were dye-marked for the first weeks and then color ringed. Chicks were called *a*- and *b*-chick according to artificial hatching order (in asynchronously hatching broods) or initial mass rank ( $\alpha$ - and  $\beta$ -chicks in even-aged twins).

Supplementary food was provided to chicks in some nests of each brood type (Table 1). Chicks were hand fed. Supplementary food consisted of freshly thawed pilchards (*Sardinops ocellata*), one of the main items in the Cape Gannet's diet (Berruti 1987). The amount of food fed (determined arbitrarily) was ca 5% of chick mass ( $\pm 25\%$  of daily food intake, calculated from hand-reared chicks (Cooper 1978). From day 5 to 40, chicks were fed small pieces of fish, and whole fish thereafter. Chick body mass was recorded every third day during the first three weeks and every fourth day thereafter until fledging. Once chicks had fledged they were caught, weighed and metal ringed (color rings were removed).

In 1987-88, 60 experimental broods were used (Table 1). Supplemental food (see above) was supplied every second day; body mass was recorded every fourth day.

### Behavioral observations

Adults were ringed and dye-marked to distinguish the members of a pair. Nests were observed unobtrusively from a distance ca 5 m at ground level or at 1.5 m height. Day-time watches of 1-14 hr were scattered throughout the chick-rearing period. A total of 1506 nest observation hours were monitored. Between 8 and 12 nests were observed simultane-

**Table 1. Experimental design and sample sizes. Experimental twins hatched 10 days apart were not considered in 1987-88.**

Breeding season	Total broods	Food supplied	One-chick broods	Two-chick broods <sup>1</sup>		
				age 0-0	age 0-5	age 0-10
1986-87	103	no	17	14	12	13
		yes	12	12	12	11
1987-88	60	no	10	10	10	—
		yes	10	10	10	—

<sup>1</sup>The notation 0-0, 0-5, and 0-10 refers to the age structure of the pairs.

ously, this was possible due to the low frequency of parental visits and chick behavior. Data collected included: frequency of chick begging bouts (*i.e.* begging sequences separated by 1 s or more) directed to either parent present at the nest; parental feeds (number of regurgitation a chick received); and number of aggressive interactions between siblings (noting the identity of the chick that initiated the attack and outcome).

The frequency of parental feeds per begging is the 'success rate'. It was calculated from the number of parental feeding received per chick as a percentage of the number of begging incidents per chick. In cases where two siblings begged simultaneously, the proportion of cases where one obtained food prior to another is the 'priority ratio' (after Fujioka 1985a).

#### Data analysis

I fitted sigmoid curves to growth data using the Derivative-free Nonlinear Regression Program of the BMDP statistical package (Ralston 1988). The models fitted were:

$$\text{Logistic: } M' = A/(1 + \exp(-K(T - I)));$$

$$\text{Gompertz: } M' = A \exp(-\exp(K(T - I))); \text{ and}$$

$$\text{von Bertalanffy: } M' = A/(1 - \exp(-K(T - I))).^3$$

Where  $M'$  is the predicted mass (g),  $A$  is the asymptote (g),  $K$  is the growth rate ( $\text{day}^{-1}$ );  $I$  is the inflection time (days); and  $T$  is the time or chick age (days). I used the distribution of the residuals over time as a criteria to choose among the three models (*cf* Zach *et al.* 1984).

To evaluate the growth performance of chicks, I considered the following variables: the parameters ( $A$ ,  $K$  and  $I$ ) of best fit model; maximum mass attained by chicks regardless of age; age at which maximum body mass was attained; fledging mass; and chick-rearing period. All variables were analyzed for the simultaneous effect of year, brood-type and food supplementation with a three-way analysis of variance (ANOVA).

Behavior of chicks was analyzed using the one-way analysis of covariance (ANCOVA) for unbalanced designs. Chick age was used as covariate. Results reported were adjusted for the covariate by  $Y_j - b_w(X_j - X_{..}) = Y_{j \text{ adj}}$ . Where  $Y_{j \text{ adj}}$  = adjusted mean for  $j^{\text{th}}$  treatment group;  $Y_j$  = unadjusted mean for  $j^{\text{th}}$  treatment group;  $X_j$  = covariate mean for  $j^{\text{th}}$  treatment group;  $X_{..}$  grand covariate mean; and  $b_w$  = pooled within-group regression coefficient (Huitema

1980). Analysis were done using the SAS statistical package (SAS 1985).

I used the G-statistic (Sokal and Rohlf 1969) to test for independence in frequency tables. Variations about means are given as  $\pm 1$  standard error.

## RESULTS

### Breeding success

There were no significant differences in the mean number of chicks fledged per nest between birds provided with supplementary food ( $0.78 \pm 0.07$ ,  $N = 78$ ) and controls ( $0.72 \pm 0.07$ ,  $N = 85$ ) ( $P > 0.5$ , randomization test). Singletons and  $0_{-10}$ twins were slightly less productive than  $0_{-0}$ twins and  $0_{-5}$ twins. In 1986-87  $0_{-0}$ twins provided with food produced significantly more chicks than singletons (both food-provided and control) ( $P < 0.05$ , randomization test). This difference was not significant in 1987-88 ( $P > 0.05$ , randomization test; Table 2).

The number of chicks fledged was significantly different among brood types ( $G_3 = 9.18$ ,  $P < 0.05$ ), *a posteriori* multiple comparisons revealed significant differences in survival rates only between singletons and  $0_{-10}$ twins. There were no statistically significant differences in the number of partial broods fledged ( $G_2 = 0.29$ ,  $P > 0.5$ ) and the number of nests with complete nest failure ( $G_2 = 1.25$ ,  $P > 0.5$ ); (Table 3).  $0_{-10}$ twins did not fledge full broods, however  $0_{-0}$ twins and  $0_{-5}$ twins fledged a similar proportion of full broods ( $G_{\text{adj},1} = 1.28$ ,  $P > 0.5$ ). The ratio of partial broods fledged to complete nest failure was similar for all twins ( $G_2 = 0.6$ ,  $P > 0.5$ ).

### Chick mortality

Nestling mortality was similar for both food-supplemented and control pairs ( $\chi^2 = 1.9$ ,  $df = 1$ ,  $P > 0.1$ , Fig. 1). Mortality

**Table 2. Breeding success of Cape gannets according to: (A) brood-type, food supplementation and year; (B) brood-type and food supplementation; and (C) overall mean for brood-types. Figures are mean number of chicks fledged per nest ± standard error and (number of nests).**

		Brood-type			
		Singletons	0-0Twins	0-5Twins	0-10Twins
A. Food	Year				
Control	1986-87	0.65 ± 0.12 (17)	0.86 ± 0.12 (14)	0.83 ± 0.21 (12)	0.45 ± 0.16 (11)
	1987-88	0.80 ± 0.13 (10)	0.90 ± 0.28 (10)	0.50 ± 0.22 (10)	no data <sup>1</sup>
Supplemented	1986-87	0.67 ± 0.14 (12)	1.33 ± 0.19 (12)	0.83 ± 0.21 (12)	0.46 ± 0.14 (13)
	1987-88	0.70 ± 0.15 (10)	0.70 ± 0.26 (10)	0.80 ± 0.20 (10)	no data <sup>1</sup>
B. Food					
Control		0.70 ± 0.09 (27)	0.88 ± 0.16 (24)	0.68 ± 0.15 (22)	0.45 ± 0.16 (11)
Supplemented		0.68 ± 0.10 (22)	1.05 ± 0.17 (22)	0.82 ± 0.14 (22)	0.46 ± 0.14 (13)
C. Overall mean		0.69 ± 0.07 (49)	0.96 ± 0.12 (46)	0.75 ± 0.10 (44)	0.46 ± 0.51 (24)

<sup>1</sup>0-10twins were not set up in 1987-88.

was higher during the first 20 days (14-23%) and was mainly due to mortality of the younger chick added to the nest, especially when the age difference between nestlings in a brood was 5 or 10 days. Mortality decreased significantly with chick age ( $\chi^2 = 39.8$ ,  $df = 7$ ,  $P < 0.005$ ). A total of 159 (out of 273, 58.2%) chicks died during the nestling period. Of these, at least 75% died, presumably, by starvation.

**Chick growth and parameters of growth model**

Although the Gompertz model over- and sub-estimated chick mass at different times of development, it did so in a less pervasive manner than the Logistic and von Bertalanffy models (Fig. 2), providing the least biased description of body mass growth of Cape Gannet chicks.

The average mass of chicks at hatching was  $69.9 \pm 1.2$  g ( $N = 39$ ), about 71.5% of

the fresh egg mass ( $97.8 \pm 0.8$  g,  $N = 86$ ) and *ca* 2.3% of the adult mass ( $3106 \pm 25$  g,  $N = 101$ ). Growth was slow during the first 10-12 days of life, and fast and almost linear up to 50-58 days. The rate of mass gain slowed down thereafter until body mass reached its maximum value about 80 days after hatching. Body mass dropped to *ca* 88% of the peak mass by the time of fledging.

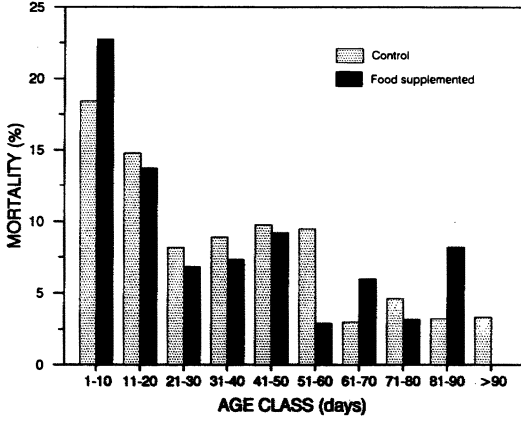
Variation in the parameters of growth model are illustrated in Fig. 3. Chicks had a significantly higher growth rate during 1987-88 than during 1986-87 ( $F_{y[1,99]} = 8.71$ ,  $P < 0.01$ ), whereas the asymptote was higher in 1986-87 than in 1987-88 ( $F_{y[1,99]} = 6.03$ ,  $P < 0.05$ ). Inflection time was not significantly different between years ( $F_{y1,99} = 3.25$ ,  $P > 0.07$ ). Differences among brood-types were significant for inflection time ( $F_{b[2,99]} = 3.29$ ,  $P < 0.05$ ), but not for growth rate ( $F_{b[2,99]} = 0.8$ ,  $P > 0.4$ ) and asymptote ( $F_{b[2,99]} = 0.57$ ,  $P >$

**Table 3. Comparison of reproductive success (% in parenthesis) of singletons and experimental twins, years and food treatments pooled.**

	Singleton	0-0twins	0-5twins	0-10twins
A. No. nests	49	46	44	24
B. No. chicks fledged <sup>1</sup>	34 (69.2)	44 (47.8)	33 (37.5)	11 (22.9)
C. No. nests fledging:				
1. Full broods <sup>2</sup>		13 (28.3)	6 (13.6)	0 (0)
2. Partial broods <sup>2</sup>		18 (39.1)	21 (47.7)	11 (45.8)
3. Complete nest failure <sup>2</sup>	15 (30.6)	15 (32.6)	17 (38.6)	13 (54.2)

<sup>1</sup>% of number of chicks in each brood type.

<sup>2</sup>% of number of nests in each brood type.

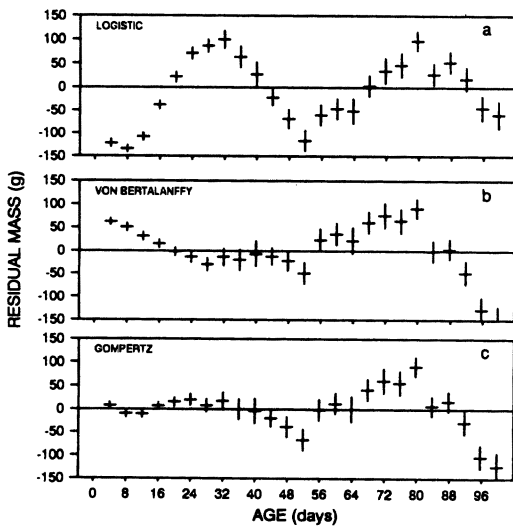


**Figure 1.** Chick mortality of control and food supplemented chicks (brood-types and years pooled). Mortality corresponds to the percentage of chicks dead at the end of the ten-day period with respect to those alive at the beginning of the corresponding period. Initial number of chicks were 141 and 132 for control and food supplemented birds respectively.

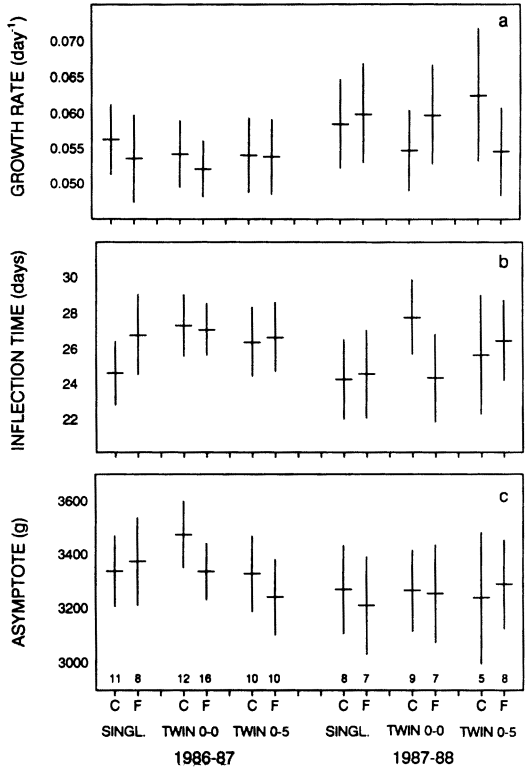
0.5). Similarly, food supplementation had no significant effect on growth rate ( $F_{f[1,99]} = 0.56, P > 0.4$ ), inflection time ( $F_{f[1,99]} < 0.01, P > 0.9$ ), and asymptote ( $F_{f[1,99]} = 0.82, P > 0.3$ ).

Maximum body mass and age at maximum mass

Maximum body mass (Fig. 4a) was significantly different among brood-types



**Figure 2.** Mean residuals and 95% confidence intervals for (a) logistic, (b) von Bertalanffy, and (c) Gompertz growth models fitted to body mass of 113 Cape Gannet nestlings.



**Figure 3.** Parameters of Gompertz growth model (mean  $\pm$  95% confidence interval) according to year, brood-type and food supplementation. (a) growth rate, (b) inflection time, and (c) asymptote.

( $F_{b[2,99]} = 3.59, P < 0.05$ ) and food treatments ( $F_{f[1,99]} = 4.02, P < 0.05$ ), but not of year ( $F_{b[1,99]} = 1.39, P > 0.2$ ). Control chicks attained a higher peak mass ( $3376 \pm 25, N = 55$ ) than food-supplemented chicks ( $3287 \pm 25, N = 56$ ). The age at maximum body mass (Fig. 4b) was statistically similar between years ( $F_{y[1,99]} < 1, P > 0.5$ ), food treatments ( $F_{f[1,99]} < 1, P > 0.8$ ), and brood-types ( $F_{b[2,99]} < 1, P > 0.4$ ).

Fledging mass and chick-rearing period

Differences between mean fledging mass (Fig. 5a) of chicks that received additional food ( $2984 \pm 48$  g,  $N = 52$ ) and controls ( $3017 \pm 31$  g,  $N = 53$ ) were not statistically significant ( $F_{f[1,99]} < 1, P > 0.6$ ), nor were differences between broods ( $F_{b[2,93]} < 1, P > 0.5$ ). However, differences between years were highly significant ( $F_{y[1,99]} = 21.55, P < 0.001$ ): overall mean for 1986-87 was  $3082 \pm 25$  g ( $N = 62$ ) and for 1987-88 was  $2883 \pm 33$  g ( $N = 43$ ).

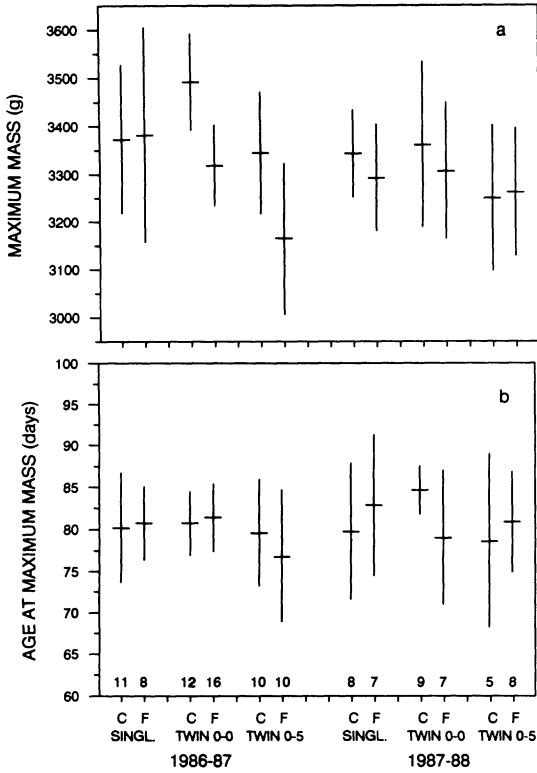


Figure 4. Mean and 95% confidence interval for maximum mass attained by chicks (a) and age at maximum mass (b) for the different treatments. C and F are control and food supplemented chicks respectively. Numerals are sample sizes.

Differences in chick-rearing period (Fig. 5b) were not significant between years ( $F_{y[1,93]} < 1, P > 0.4$ ), food treatment ( $F_{f[1,93]} < 1, P > 0.5$ ), or brood-type ( $F_{b[2,93]} = 2.28, P > 0.1$ ).

Growth of twins

In all twinned broods where both chicks fledged (years pooled, incomplete broods excluded for this analysis), the body mass of *a*-chicks was significantly higher than that of *b*-chicks ( $P < 0.05$ ), at equivalent ages, during the first four weeks of development and at 56 days old (Fig. 6). There were no significant differences in body mass of twins provided with extra food and controls. None of the growth parameters studied showed significant effects due to hatching order or food addition (Table 4), except that maximum mass was significantly higher in controls than in experimental chicks, irrespective of their rank.

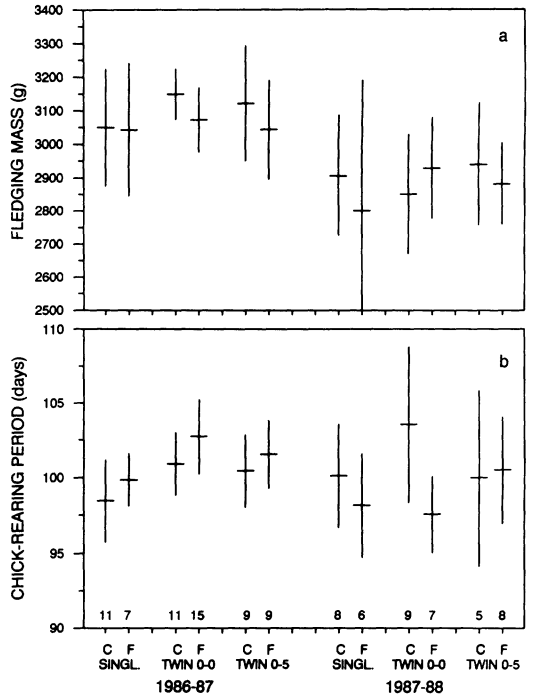


Figure 5. Mean and 95% confidence interval for fledging mass (a) and chick-rearing period (b) for the different treatments. C and F are control and food supplemented chicks respectively. Numerals are sample sizes.

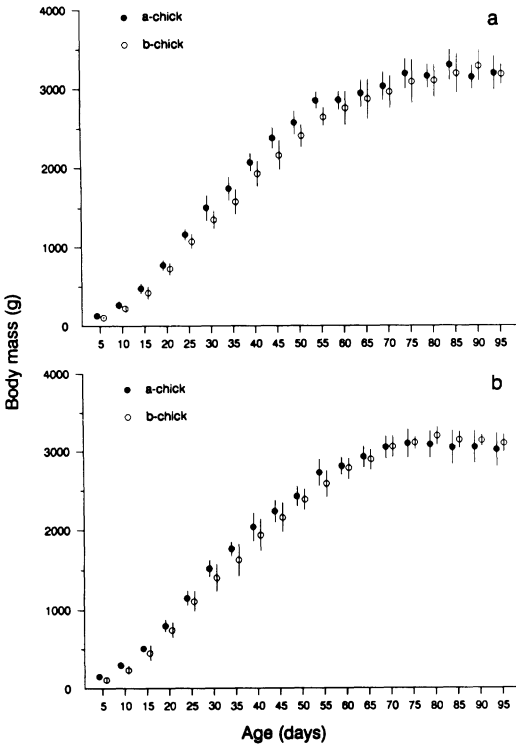
Behavioral observations

There was a trend to increased begging frequency from singletons to  $_{0.0}$ twins and to  $_{0.5}$ twins, but the means were not significantly different. Begging frequency increased significantly with chick age (Table 5).

The number of parental feedings ( $\text{day}^{-1} \text{ chick}^{-1}$ ) were significantly different among broods: singletons were fed more often than  $_{0.0}$ twins and  $_{0.5}$ twins, but parents of twins fed their chick at the same rate. Parental feedings to chicks decreased significantly with chick age (Table 5).

Success rate decreased as growth of nestlings proceeded. Singletons had a success rate almost twice those of twins, however the large variation around the means made these differences non-significant (Table 5).

The begging frequency was similar between chicks in  $_{0.0}$ twins (Wilcoxon two-sample test,  $U_{15,15} = 125, P > 0.1$ ) and  $_{0.5}$ twins ( $U_{6,6} = 20, P > 0.1$ ). The number of parental feeding that *a*- and *b*-chicks received were similar ( $U_{16,16} = 145, P > 0.1$ ).



**Figure 6.** Average mass and 95% confidence interval of siblings in broods where both chicks fledged, for (a) control (N = 9) and (b) food supplemented birds (N = 10). Hatching order is *a*- first and *b*-chick second, in even-aged twins *a*-chick is the heaviest hatchling.

for  $_{0.0}$ twins; and  $U_{6,6} = 27, P > 0.1$  for  $_{0.5}$ twins). Similarly, the success was not significantly different between chicks of  $_{0.0}$ twins ( $U_{15,13} = 111, P > 0.1$ ) and  $_{0.5}$ twins ( $U_{6,6} = 28, P > 0.05$ ; Table 6).

Priority ratios between *a*- and *b*-chicks of  $_{0.0}$ twins (58:43) and between  $\alpha$ - and  $\beta$ -chicks of  $_{0.5}$ twins (15:8) were not statistically different (Fisher's exact test,  $P = 0.658$ ). In  $_{0.0}$ twins a similar proportion of non-competitive feeding took place between *a*- and *b*-chicks (88:78,  $G_{adj,1} = 0.49, P > 0.3$ ), but not in  $_{0.5}$ twins (20:0), where non-competitive feeding of *b*-chicks were not observed (though they may occur).

Sibling aggression usually consisted of weak pecking (without causing injuries) and generally did not elicit an aggressive response from the chick being attacked, even if it was dominant. In  $_{0.0}$ twins, where the dominance rank at hatching was frequently reversed during the development period, the frequency of aggressive encounters won by *a*-chicks and by *b*-chicks (66:58) were not significantly different ( $G_{adj,1} = 0.395, P > 0.5$ ). This situation was quite different in  $_{0.5}$ twins, where the  $\alpha$ -chick more frequently attacked the  $\beta$ -chick (33:10,  $G_{adj[1]} = 11.81, P < 0.005$ ), a complete reversal of the dominance hierarchy during the nesting period was not observed in  $_{0.5}$ twins.

**Table 4.** Growth parameters of artificial twins where both chicks fledged, and results of two-way ANOVA. Hatching order is *a*- first and *b*-chick second, in even aged twins *a*-chick is the heaviest hatchling.

Variate	Control		Food supplied	
	<i>a</i> -chick N = 9	<i>b</i> -chick N = 9	<i>a</i> -chick N = 10	<i>b</i> -chick N = 10
<b>A. Growth parameters</b>				
Maximum mass (g)	3428 ± 59	3372 ± 93	3270 ± 53	3240 ± 66
Age at maximum mass (days)	80 ± 2.3	82 ± 2.9	80 ± 2.4	74 ± 2.3
Fledging mass (g)	3000 ± 100 <sup>1</sup>	3027 ± 67	3014 ± 57 <sup>2</sup>	2950 ± 55
Chick-rearing period (days)	103 ± 1.5 <sup>1</sup>	103 ± 1.7	101 ± 1.1 <sup>2</sup>	102 ± 1.5
<b>B. Two-way ANOVA</b>				
	F-values and significance level			
	Main factors		Interaction	d.f.
Variate	Food supplied	Hatching order	F × H	
Maximum mass	4.45*	0.39 <sup>ns</sup>	0.03 <sup>ns</sup>	1, 34
Age at maximum mass	3.05 <sup>ns</sup>	0.41 <sup>ns</sup>	2.37 <sup>ns</sup>	1, 34
Fledging	0.20 <sup>ns</sup>	0.07 <sup>ns</sup>	0.44 <sup>ns</sup>	1, 32
Chick-rearing period	0.98 <sup>ns</sup>	0.13 <sup>ns</sup>	0.47 <sup>ns</sup>	1, 32

<sup>1</sup>N = 8.

<sup>2</sup>N = 9.

\* =  $P < 0.05$ .

<sup>ns</sup> = not significant,  $P > 0.05$ .



**Table 5. Number of acts of begging food by chicks and number of parental feedings in singletons, 0-0twins and 0-5twins. (A) means adjusted for the covariate; and (B) analysis of covariance, with chick age as covariate. Figures are mean  $\pm$  SE (day<sup>-1</sup> chick<sup>-1</sup>) and sample size (chick $\cdot$ day). Only all-day observations are included.**

	Begging frequency		Parental feeding		Success rate (%)		N
A. Cell means							
Singles	50.2 $\pm$ 13.6		4.2 $\pm$ 0.5		10.0 $\pm$ 2.4		34
0-0twins	77.6 $\pm$ 11.1		2.9 $\pm$ 0.4		5.6 $\pm$ 1.9		48
0-5twins	89.4 $\pm$ 12.1		2.0 $\pm$ 0.4		4.0 $\pm$ 0.4		40
Total <sup>1</sup>	73.9 $\pm$ 7.1		3.0 $\pm$ 0.3		6.3 $\pm$ 1.2		122
B. ANCOVA table							
Effect	F	P	F	P	F	P	d.f.
Brood	2.31	0.104	5.35	0.006	1.78	0.173	2, 118
Covariate	10.21	0.002	4.74	0.031	6.31	0.013	1, 118

<sup>1</sup>Non-adjusted means.

The aggression rate (number of aggressive encounters per hour per brood) was similar for 0-0twins (0.30, 410.68 nest-hour) and 0-5twins (0.33, 131.42 nest-hour; *t*-test to compare two proportions, *t*<sub>s</sub> = 0.53, *P* > 0.4, Sokal and Rohlf 1969).

## DISCUSSION

### Chick growth and twinning experiments

Cape Gannet chicks grew rapidly, achieving a 42-fold increase in body mass in the first 2 months of life. This growth-rate is faster than that calculated from Jarvis (1974) for the same species, but comparable to that reported by Montevecchi *et al.* (1984) for Northern Gannets, and identical to that of hand-reared Cape Gannet chicks (Cooper 1978).

Control chicks, both singles and twins, grew at the same rate as food-supplemented chicks, and no significant differences in fledging mass, chick-rearing period, peak mass, and age at peak mass were found. These results indicate that chicks were raised under favorable food conditions during the two breeding seasons studied here. The results also suggest that chicks regulate their food intake, be-

cause, contrary to predictions, supplementary food did not result in increased body mass or fledging mass. As similar response to additional food has been reported by Wehle (1983) for Tufted and Horned Puffins, and by Ricklefs *et al.* (1987) for Leach's Storm-petrels (*Oceanodroma leucorhoa*). In both studies, regulation of food intake by chicks and high food availability were invoked as possible explanations. The fact that Cape Gannets were able to raise two chicks is a clear indication that they responded to the increased food demand at the nest. However, some seabirds deliver food to the nest independently of the food demand (Ricklefs 1987).

The growth rate, chick-rearing period and fledging mass of control chicks in Jarvis's (1971, 1974) study are below the 95% confidence interval chicks in the present study (Table 7). This suggests that the food availability was lower during 1966-68 (Jarvis's study period) than in 1986-88. Similarly, between year differences in breeding success and fledging mass suggest that food availability was higher in 1986-87 than during 1987-88.

Cape Gannets have successfully raised artificially twinned broods in four breed-

**Table 6. Number of acts of begging food by chicks, number of parental feedings and success rate of chicks in 0-0twins and 0-5twins. Figures are frequency day<sup>-1</sup>  $\pm$  SE and (sample size).**

	0-0Twins		0-5Twins	
	a-chick	b-chick	$\alpha$ -chick	$\beta$ -chick
Begging frequency	96.4 $\pm$ 17.8 (15)	89.3 $\pm$ 20.2 (15)	152.2 $\pm$ 54.8 (6)	171.8 $\pm$ 42.2 (6)
Parental feedings	4.3 $\pm$ 0.8 (16)	3.3 $\pm$ 0.6 (16)	3.2 $\pm$ 0.9 (6)	1.3 $\pm$ 0.6 (6)
Success rate	14.9 $\pm$ 7.1 (15)	4.7 $\pm$ 1.1 (13)	2.1 $\pm$ 0.6 (6)	0.8 $\pm$ 0.4 (6)

**Table 7. Comparisons of growth parameters of chicks during the present study with those from Jarvis' (1971) study.**

Growth parameter	Present study 95% conf. int. <sup>1</sup>	Jarvis' study (1971)
Asymptote (g)	3275 – 3351	3378 <sup>2</sup>
Growth rate (day <sup>-1</sup> )	0.054 – 0.057	0.050 <sup>2</sup>
Inflection time (days)	25.6 – 26.4	26.9 <sup>2</sup>
Chick-rearing period (days)	99.8 – 101.4	97.2
Fledging mass (g)	2956 – 3044	2895 <sup>3</sup>

<sup>1</sup>N = 114; fledging mass: N = 103.

<sup>2</sup>From model fitted to figures of Table 33, Jarvis (1971).

<sup>3</sup>N = 1004.

ing seasons: two in Jarvis' study (1971, 1974) and two during the present study. However, Jarvis' twins fledged at significantly lower mass than singletons. The immediate post-fledging survival in Cape Gannets is affected by the fledging mass (Jarvis 1974), and these twins apparently had a higher mortality than singletons. In contrast, during the present study period the fledging mass of twinned chicks did not differ from that of singletons (and at least during 1986-87 chick fledging mass was significantly higher than Jarvis' figure). Therefore, it is probable that post-fledging survival of twins during 1986-88 was similar to that of singletons.

### Behavioral observations

Large size disparity and asymmetry of competitive ability in food contests often result in starvation of junior sibs (Fujioka 1985b, Cash and Evans 1986, Drummond *et al.* 1986, Mock and Ploger 1987). Sibling dominance hierarchies were very slight in  $0_{-0}$ twins and were frequently reversed during the nesting period, whereas in  $0_{-5}$ twins the dominance hierarchies were more stable. This asymmetry was reflected in food contests, in which the subordinate chick had a significantly lower priority ratio, whereas in  $0_{-0}$ twins both chicks had similar priority ratios. These factors suggest that if brood reduction occurs it will do so by starvation through food contests. In fact, starvation is thought to be the main cause of death during the nestling period. Siblicide aggression was never observed.

Cape Gannet pairs raising twins were able to increase feeding rates to cope with the additional food demand imposed by

the extra chick. However, the feeding rate per chick in twins was lower than the feeding rate of singles. This suggests that parental optimal feeding effort is somewhat lower than the optimum food demanded by chicks. This reflects Triver's (1972) parent-offspring conflict in which twinned chicks have to beg longer than singles to be fed. Parents of twins, and particularly parents of  $0_{-5}$ twins, seem to be conservative in their parental effort during a particular breeding season, this may help to avoid a negative energy balance which might endanger their future breeding success. A similar result has been reported for natural asynchronously hatching broods of the Cattle Egret (*Bubulcus ibis*), (Fujioka 1985a).

Hussell's (1972) demand reduction hypothesis predicts that parents of asynchronously hatching broods will experience a higher breeding success by spreading out the feeding demands of the brood. This prediction does not hold for the results of the present study: breeding success of  $0_{-0}$ twins tended to be higher than in  $0_{-5}$ twins, though the difference was not significant. However, the mechanism for this hypothesis to operate, *viz.* reduced food demand, does seem to occur in  $0_{-5}$ twins. If the number of parental-nest visits with food delivered to chicks and the number of parental feeding can be used as an estimate of parental investment, then it is clear that pairs of  $0_{-5}$ twins reduced their feeding effort to a value between that of parents of singletons and that of  $0_{-0}$ twins. It can then be expected that, under less favorable conditions, parents of  $0_{-5}$ twins might have a better chance to fledge two chicks: proportionally they can increase their feeding effort more than pairs of  $0_{-0}$ twins.

It has been shown that the main hypotheses concerning hatching patterns do not hold for experimental twins in Cape Gannets. However, some of the results indicate that brood reduction may operate under poorer food availability. In addition, the behavioral mechanisms of demand reduction in 0.5twins are present and they may confer an additional advantage to them under less favorable conditions. For this reason twinning experiments should consider synchronously and asynchronously hatching broods to allow the mechanisms of brood reduction and demand reduction hypotheses to operate.

### Population regulation

Ashmole's (1963) hypothesis predicts that increased competition for food around the colony will reduce the reproductive output of tropical seabirds long before having an affect on adult mortality, and consequently less efficient individuals will be prevented from rearing young. A necessary condition for satisfying Ashmole's hypothesis is that competition for food affects population growth (by lowering the reproductive output) and that consumption of food affects food availability. However this does not seem to be the case in the Benguela region, where seabirds consume about 5.8% of the estimated fish production, of which only a fraction can be attributed to Cape Gannets as they account for 19.4% of the overall biomass of seabird residents in the southern Benguela region (Duffy *et al.* 1987).

This study does not support Ashmole's hypothesis that food availability during the breeding season is a factor limiting both chick growth and breeding success. Neither does it confirm nor contradict Lack's (1966) hypothesis, at least for the food conditions prevalent during the study period.

Populations, rather than precisely tracking variations in resource levels, have a lagged response to such changes. Non-coincidence of many of the factors involved in resource systems may also reduce the match of populations to resources, and stochastic factors further distort the relationship. Consequently, although populations may at times be limited by resource availability, resources may be superabun-

dant at other times (Wiens 1984). Resource availability influences both individual reproduction and density-dependent limitation of population size. It is possible, therefore, that individual reproductive output is limited by feeding rate, specifically by the ability of birds to obtain enough food for themselves and their offspring. Population size, however, may be set by other resources (such as available nesting-space, Thomson 1980) and high mortality during El Niño-like events (Duffy and Siegfried 1987).

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