

Chapter 18

Breeding in a dynamic system: intra- and inter-seasonal variability in foraging behaviour and chick growth of Cape Gannets

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Foraging in a highly dynamic system requires flexibility of breeding animals. Intra-seasonal fluctuations in food abundance and distribution during the chick rearing period will affect the foraging behaviour of parents and consequently breeding performance within the breeding season. Foraging behaviour and chick growth of Cape Gannets (*Morus capensis*) breeding at Malgas Island (South Africa) in the Benguela upwelling ecosystem was investigated during the breeding seasons of 2003/04 and 2004/05. Trip duration varied by as much as 6–8 hrs between the beginning and the end of the same season, without any apparent seasonal trend. In 2003/04 feeding trips were longer later in the season, whereas the opposite occurred in 2004/2005. The time spent flying during foraging trips differed significantly within the second season, decreasing by 37% from 10.7 hrs to 6.8 hrs be-

tween the first and second half of the season. Large intra-seasonal variation in the growth of the chicks was found in both seasons and growth was 28.6% faster in the first season compared to the second. The slower growth in the second season was associated with a decrease in the proportion of two prey species with high calorific contents, anchovies (*Engraulis encrasicolus*) and sardines (*Sardinops sagax*), in the diet (from 58.7% to 23.8% wet mass). The decreased growth rate of the chicks was also associated with a decrease in fledging success (36.6% compared to 54.5%). Breeding in a dynamic system like the Benguela upwelling ecosystem generates large variation in breeding performances, indicating the importance of studying intra-seasonal variation besides inter-seasonal comparisons.

Keywords: foraging effort, growth performance, diet, variability, *Morus capensis*, Benguela upwelling system

Introduction

Reproductive parameters such as the timing of breeding and breeding success are strongly linked to food availability (Lack 1968, Martin 1995). In small passerine birds the timing of breeding is crucial because of the strong relationship between the peak in food supply and fledging success (e.g. Verboven et al. 2001, Tremblay et al. 2003). In seasonal environments, both food availability per se and the predictability of food abundance seem to be crucial for breeding (Siikamäki 1998). Seabirds however, frequently forage in a highly patchy and dynamic habitat characterised by fluctuations in prey distribution, availability and abundance throughout the breeding season (Crawford 1999, Suryan et al. 2002, Weeks et al. 2006). The effects of such variability in food supply on breeding success may be amplified by the prolonged chick rearing period which is typical of seabirds (Lack 1968), resulting in a long breeding season in a dynamic environment. Rather than expecting a particular seasonal direction in breeding performance, the fluctuating food resources of seabirds will affect foraging behaviour and breeding parameters on a more short-term scale (Shea & Ricklefs 1985; Le Corre et al. 2003).

Most seabird species are central place foragers, commuting considerable distances from their breeding colony to feeding areas and returning with food for their offspring (Orians & Pearson 1979). Adults have to support the increasing energy demand of their chicks, and at the same time

cope with any sudden changes in the distribution, abundance or composition of prey. To negotiate such changes successfully, they need to alter their foraging behaviour in space and time. Seabirds are able to adjust their time spent away from the colony (Charrassin et al. 1999; Dall'Antonia et al. 2001), make different allocation decisions (Takahashi et al. 2003) or catch different prey species (Berrow & Croxall 2001). Flexibility in foraging behaviour is an essential adaptation for when feeding conditions change within the breeding season (Granadeiro et al. 1998). Additionally parents have to meet the increasing chick's energy requirements, which put large energetic demands on the parents (e.g. Birt-Friesen et al. 1989; Adams et al. 1991), especially when food is scarce. Chick rearing parents are restricted by their maximum working capacity (Drent & Daan 1980) above which they do not increase their foraging effort, therefore boundaries are set to energetic flexibility. Because periods with low food abundance will negatively affect chick growth, this parameter can be a useful indicator of local food availability (Ricklefs et al. 1984, Adams et al. 1992).

Seabird breeding numbers are closely associated with prey availability (Monaghan et al. 1989) and therefore islands in the vicinity of upwelling systems are characterised by large numbers of breeding seabirds. Prey species are particularly abundant in these systems (Brown & Gaskin 1986; Wolanski & Hamner 1988) on account of the high rates of primary production sustained by the upwelling of nutrient-rich waters. However, fluctuations in prey abundance associated with

variation in the location and intensity of the upwelling cells within and between years (Crawford 1999; Demarcq et al. 2003) can have considerable effects on breeding conditions for seabirds (Montevecchi & Myers 1995; Suryan et al. 2002). For example, the Benguela Current upwelling system on the west coast of southern Africa is wind driven and therefore upwelling can stop when the wind drops. Furthermore, in the southern Benguela, there have been large-scale distributional shifts in the populations of sardines (*Sardinops sagax*) and anchovies (*Engraulis encrasicolus*) (van der Lingen et al. 2005). These species are high in calorific content (Batchelor & Ross 1984) and are favoured prey of several seabird species, including the Cape Gannet (*Morus capensis*).

The Cape Gannet is one of the most abundant locally breeding seabirds in the Benguela ecosystem. At Malgas Island (Saldanha Bay, South Africa) the breeding season of the gannet colony lasts eight to nine months (pers. obs.); although individual breeding attempts are 4–5 months long if successful (c. 42 days of incubation and c. 110 days to raise a chick), there is inter-individual variation of up to several months in the onset of breeding. Together, the long breeding season of the Cape Gannet and the dynamic nature of the Benguela system (Weeks et al. 2006) are ideal circumstances to study the responses by a breeding seabird population to temporal changes in the environment. Therefore, using measures of chick growth and adult foraging behaviour, the aim of this study was to investigate how Cape Gannets cope with the challenges of breeding in a fluctuating environment.

Material and Methods

During the 2003/2004 and 2004/2005 breeding seasons, the gannet colony at Malgas Island (33°02'S, 17°55'E) was visited every alternate week between early October and late February, for a week at a time. The same study protocol was followed during each week of fieldwork.

Foraging behaviour of adults

The foraging behaviour of the gannets was studied using GPS-dataloggers (Newbehavior; Zürich, Switzerland), which recorded the speed and geographic position of a deployed bird at 10 sec intervals (c. 10 m resolution). The loggers were sealed in two waterproof bags; total weight was about 50 g, less than 2% of the adult body mass (2605 g in this study). Birds with different feeding objectives (i.e. chicks of different age and size) were selected as study animals. The devices were deployed when the birds left the nest for a foraging trip, which always occurred once the chick was attended by the other parent to correct for different trip durations when chicks are left unattended (Lewis et al. 2004). The departing bird was caught with a hooked pole, measured and weighed. A logger was attached to its tail feathers with waterproof Tesa®-tape (Beiersdorf AG, Hamburg), which does not damage the tail feathers, and the bird was released near its nest. The procedure took c. 5 min and most birds left the colony within minutes after deployment. The same devices were deployed on Cape Gannets during a previous research project, with no obvious adverse effects on the behaviour of the birds (Gremillet et al. 2004). A couple of hours after deployment (to allow for digestion of the food obtained from the returned parent), the chick was measured for bill length (to 0.1 mm), wing length (to 1 mm) and body mass (to 5 g below 1 kg; to 25 g above 1 kg). The nest was then monitored hourly until the parent with the logger returned, whereupon the logger was retrieved by re-capturing the bird and taking off the tape and logger.

The following behaviour types were recognised from the GPS data recovered from the loggers: out-flight, search-flight, time spent drifting, fishing events, return-flight, total distance covered and duration of the foraging trip. From these data we calculated flying time (total duration minus time spent drifting) and foraging time (search flight plus fishing events). Flying time was taken as an indicator for the foraging effort, affecting parent's allocation decisions, while the foraging trip duration determined the feeding frequency of chicks, affecting chick growth.

Chick growth

Access to the centre of the colony involved unacceptable levels of disturbance; therefore only chicks near the periphery of the colony, at four different sites, were measured for growth. Although predation pressure from kelp gulls (*Larus dominicanus*) increases towards the periphery of the colony (pers. obs.), this would not affect growth rates. The chicks were taken from the nest, measured and returned to the nest within three minutes. Bill length, wing length and body mass were measured (as above for the chicks of instrumented birds) and the number of ticks (*Ornithodoros capensis*) on each chick was counted. In order to standardize the measuring protocol, chicks were measured in the same sequence and at the same time of the day by the same person (RAN). Newly hatched chicks at the four sites were included in the measuring protocol to have data on the growth of young chicks throughout the season. The measurements continued until either the chick died or was completely feathered and ready to fledge. The same four sites were used in 2003/2004 and 2004/2005.

Growth index

Because none of the standard parametric growth models fitted the data adequately, the growth rates were analysed using a non-parametric approach developed by le Roux & Underhill (in prep), (see appendix for full description of method). This growth index represents a common currency to measure departures from "mean" growth, and is independent of whether growth measures are taken shortly after hatching, when the absolute growth rates (gd^{-1}) tend to be small, at the maximum growth spurt, when growth rates tend to be large, or late in growth, when growth rates tend to decrease. The scores are assumed to be normally distributed (which to a first approximation is probably reasonable), so that the magnitudes of z-values can be expected to be within the standard normal distribution.

Diet sampling

The diet of the gannets was sampled during 1–3 consecutive days each month by Marine and Coastal Management. Birds were captured with a hooked pole upon arrival from a foraging trip and inverted over a bucket, into which they regurgitated. Fifty samples were collected per month, each of which was analysed independently. The analyses involved identifying each species represented in the sample and then, for each prey species separately, determining its weight in the sample, the number of individuals (by counting the numbers of head and tails) and size of whole fish. From these data the relative contribution to the total diet in percentage wet mass was calculated for each species.

Data analysis

The foraging behaviour of the adults was analysed using multiple regression in which the potential explanatory effect

Table 1: *Morus capensis*. Summary statistics for foraging data obtained from GPS data-loggers for the 2003/2004 and 2004/2005 breeding seasons. Chick age is the mean age of the chicks of all deployed birds and flying time is obtained by subtracting time spent drifting on the sea-surface from total trip duration

		Chick age (days)	Duration (hrs)	Distance (km)	Flying time (hrs)	Drifting time (hrs)
2003–2004	mean	33.0	22.5	428.4	8.8	13.7
	N	74	78	78	78	78
	stdev	21.7	11.8	198.8	4.2	8.3
	min–max	0–100	3.1–50.9	77.8–933.1	1.8–18.9	0.5–35.5
	mean	32.7	23.8	455.8	9.1	14.7
2004–2005	N	82	85	85	85	85
	stdev	21.3	13.0	253.1	5.2	8.8
	min–max	0–93	3.1–54.0	101.3–1220.7	2.2–26.8	0.9–36.7

of variables was tested using a backwards deletion method. The residuals of significant models were tested for normal distribution. Growth indices were calculated using GenStat 8 and statistical analyses were done with SPSS 13.0 statistical package.

Results

Characteristics of feeding trips

GPS loggers were deployed on 224 birds during this study (99 in 2003/04 and 125 in 2004/05). One hundred and sixty three complete tracks were obtained (72.8%); the main reasons for incomplete tracks were insufficient battery power during longer foraging trips and gaps in the tracks due to communication problems between the logger and the GPS satellites. Three GPS loggers were lost, either because the bird returned without the logger, or did not return to the nest at all. Only complete tracks were used for analyses. The summary statistics of the foraging parameters are given in Table 1. All the foraging parameters were inter-related and correlations between them were positive (Table 2).

Variation in foraging behaviour

To investigate intra-annual variation in foraging behaviour, weekly means for the foraging parameters were calculated and compared. Deployment occurred during 3–4 days each week the colony was visited and the data retrieved represented foraging behaviour over 5–7 days. For each of these periods, data for a minimum of 7–19 complete foraging trips were obtained. Trip duration had a tri-modal distribution due to the effect of birds spending either zero, one or two nights at sea. Total time spent flying during the trip was normally distributed (Kolmogorov-Smirnov $Z = 1.1$, $P = 0.14$). There was no difference in flying time between seasons (One-way ANOVA: $F_{1,161} = 0.2$, $P = 0.634$), but there was a difference between periods within 2004/2005 (One-way ANOVA: 2003/04 $F_{6,71} = 1.1$, $P = 0.358$; 2004/05 $F_{5,79} = 2.4$, $P = 0.029$, Fig. 1). Trip duration did not differ between seasons (Kruskal-Wallis Test: $\chi^2 = 10.2$, $df = 12$, $P = 0.596$, Fig. 1) or between periods within seasons (Kruskal-Wallis Test: 2003/04 $\chi^2 = 6.7$, $df = 6$, $P = 0.347$; 2004/05 $\chi^2 = 3.2$, $df = 5$, $P = 0.671$). In 2003/2004, the mean trip duration decreased gradually between September and mid December, from 23.3 hrs to 18.9 hrs (overall mean = 20.5 hrs). This increased to 28.7 hrs at the end of December and the beginning of January. The trend was the opposite in 2004/2005; long foraging trips were made between the beginning of the season and the end of November (mean duration = 26.3 hrs), after which the duration decreased (mean duration = 20.0 hrs). From these results it was possible to broadly divide each season into two periods, each with different characteristics for the foraging

parameters. The division in 2003/2004 was between the first five and the two last periods (Fig. 1), whereas in 2003/2004, the six periods (one less than 2003/2004) were evenly split in the middle (Fig. 1). Parameters were then compared between the resulting four periods. Trip duration was significantly higher at the end of 2003/2004 than at the beginning, and varied significantly between 2003/2004 and 2004/2005 (Mann-Whitney: 2003/04 $Z = -2.6$, $P = 0.011$; 2004/05 $Z = -1.7$, $P = 0.096$; Kruskal-Wallis: both $\chi^2 = 9.6$, $df = 3$, $P = 0.023$). Flying time in 2004/2005 was significantly longer during the first period compared to the second period, and also differed significantly from flying time in 2003/2004 (One-way ANOVA: 2003/04 $F_{1,76} = 3.8$, $P = 0.054$; 2004/05 $F_{1,83} = 13.8$, $P < 0.0001$; both $F_{3,159} = 1.4$, $P < 0.0001$).

Growth of chicks

Growth measurements were available for 279 chicks (152 in 2003/04, 127 in 2004/05). The mean number of measurements per chick was 5.2 and the mean interval between measurements was 7.6 days (range; 5 – 42 in 2003/04, 4 – 32 in 2004/05). From these measurements 808 growth index scores were derived for 2003/2004 and 470 for 2004/2005. The mean growth (gd^{-1}) differed between the two breeding seasons (One-way ANOVA: $F_{1,1276} = 10.4$, $P = 0.001$); being 28.6% higher in 2003/2004 (mean = $32.32 \text{ } gd^{-1} \pm 32.50$) than in 2004/2005 (mean = $25.14 \text{ } gd^{-1} \pm 46.70$). After correcting for chick age, growth was still significantly different between the seasons (One way ANOVA: $F_{1,1276} = 5.0$, $P = 0.027$). Similarly, the mean growth index was significantly different between the two seasons (One-way ANOVA: $F_{1,1276} = 5.2$, $P = 0.023$), and between periods within each season (One-way ANOVA: 2003/04, $F_{17,790} = 3.7$, $P < 0.0001$; 2004/05, $F_{13,456} = 7.9$, $P < 0.0001$). The growth indices were modelled using a multiple regression with year, age, number of ticks and the hatching date as explanatory variables (Table 3). The model explained 3% of the variation found. The residuals still varied between periods in both seasons (One-way ANOVA: $F_{31,1246} = 5.8$, $P < 0.001$, Fig. 2), suggesting

Table 2: *Morus capensis*. Cross-correlations between foraging parameters of adult Cape Gannets for the 2003/04 and 2004/05 breeding seasons. For all correlations the sample size is 162 and the P -value < 0.0001

	Distance (km)	Duration (hrs)	Flying (hrs)	Foraging (hrs)
Duration (hrs)	0.883			
Flying time (hrs)	0.937	0.884		
Foraging (hrs)	0.901	0.883	0.924	
Drifting (hrs)	0.768	0.966	0.734	0.774

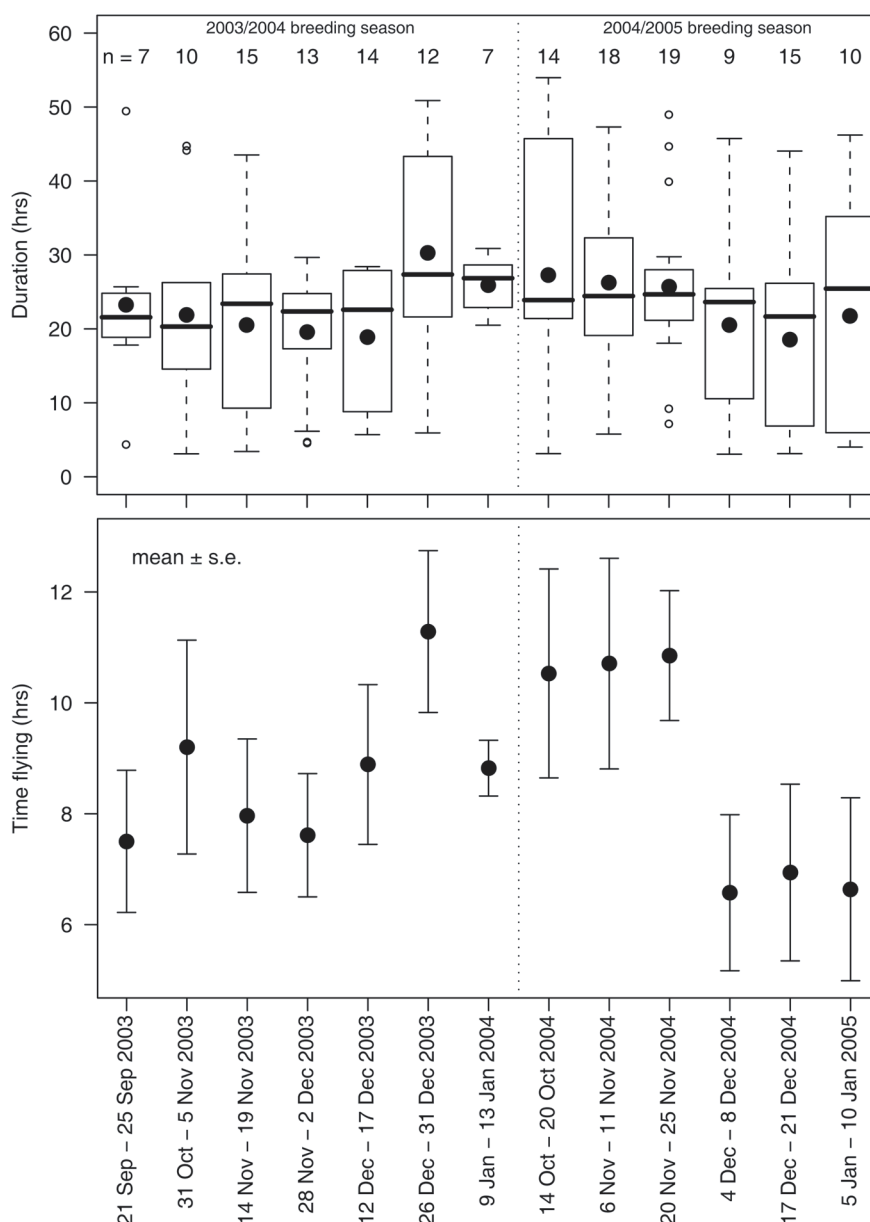


Figure 1: *Morus capensis*. (a) Box plots for trip duration (in hrs) per period for two breeding seasons (2003/04 and 2004/05). The black line indicates the median, the box the upper and lower quartiles and the error bars the extreme values. Outliers are shown by dots above the error bars. The means per period are shown by the black dots in the boxes and sample sizes are stated in top of Fig. 1 (b) Error graphs for flying time (in hrs) per period for two breeding seasons. The dots indicate the mean and the error bars the standard error

Table 3: *Morus capensis*. Results of the multiple regression with the growth index of chicks as dependent variable and year (breeding season), age (age of the chicks in days), ticks (number of ticks counted on chick) and hatching date of chick as explanatory variables

	df	Mean square	F	P
Corrected model	4	7.959	8.534	<0.0001
Intercept	1	6.259	6.711	0.0097
Age	1	22.258	23.865	<0.0001
Ticks	1	8.384	8.990	0.0028
Hatching date	1	6.219	6.669	0.0099
Year	1	4.580	4.911	0.0269
Error	1273	0.933		

that the seasonal effect was stronger than age or other effects. During 2003/2004 there was a gradual decline in growth performance with some variation between periods, but in 2004/2005 there were considerable fluctuations in scores between periods, without any particular trend being apparent. The variation in the growth index was 33.7% higher in the second breeding season ($sd = 1.15$) than in the first ($sd = 0.86$).

Foraging behaviour and chick growth

The relationship between adult foraging behaviour and chick growth was investigated by relating the means of the foraging parameters to those of chick growth for all periods (13 periods in total). The growth index was found to be signifi-

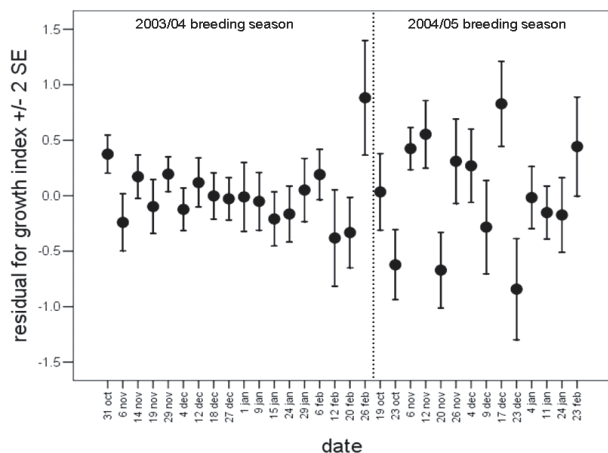


Figure 2: *Morus capensis*. The mean of the residuals from the multiple regression of the growth indices (see Table 3) per period during the 2003/2004 and 2004/2005 breeding seasons. Error bars show the standard errors. The dates on the x-axis represent the end of each period

cantly and positively correlated with total trip distance ($r = 0.59$, $P = 0.033$) and time spent flying ($r = 0.65$, $P = 0.017$, see Fig. 3) but not with trip duration ($r = 0.49$, $P = 0.093$).

Diet

In 2003/04 the main prey species during our study period was sardines (35.5%), whereas saury (*Scorpaenopsis scorpaenoides*) dominated in the next breeding season (42.1%). The relative contribution of sardines and anchovies in 2003/2004 was more than twice that of 2004/2005 (58.7% and 23.8% respectively), though intra-seasonal trends in the importance of these species differed between the two seasons (Table 4). The amount of hake (*Merluccius capensis* and *M. paradoxus*) in the diet increased by 143% between the two seasons and saury 37% (Fig. 4).

Discussion

The ability of parents to alter their foraging behaviour rapidly in space and time is a fundamental trait in the life history of seabirds (e.g. Granadeiro et al. 1998). Fluctuating environments, patchy prey distribution and increased energy demands of the offspring during growth force seabirds to adapt their time allocation and/or modify their feeding strategies (Charrassin et al. 1999; Berrow & Croxall 2001; Dall'Antonia et al. 2001). Cape Gannets breeding in the Benguela ecosystem are faced with substantial variation in prey availability within and between years (Crawford & Dyer 1995; Crawford 1999). In this study we looked at the responses of Cape

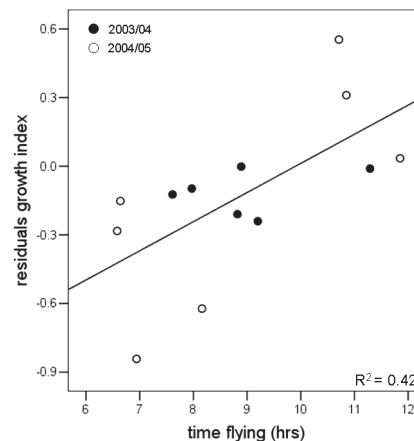


Figure 3: *Morus capensis*. Correlation between the residuals from the multiple regression of the growth indices (see Table 3) and the time spent flying (in hrs) per period during the 2003/2004 (●) and 2004/2005 (○) breeding seasons

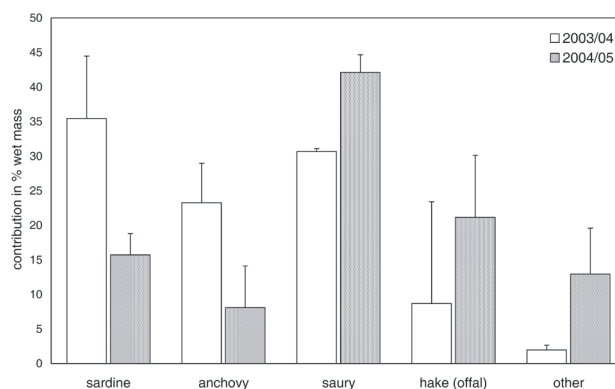


Figure 4: Bars represent the contribution in percentage wet mass per fish species to the diet of Cape Gannets for two breeding seasons from October until February. Shown are sardine (*Sardinops sagax*), anchovy (*Engraulis encrasicolus*), saury (*Scorpaenopsis scorpaenoides*), hake (*Merluccius capensis* and *M. paradoxus*) and other species, in order of decreasing energetic content (Batchelor & Ross 1984). Error bars show the standard error

Gannets to fluctuating conditions during two consecutive breeding seasons. The results show that foraging behaviour, diet and growth of the chicks can all vary drastically within the extended breeding season.

Changes in food availability

Diet samples of seabirds have been used as indicators for local food availability (Monaghan et al. 1989; Crawford 1999;

Table 4: Monthly contributions of prey species in percentage wet mass per fish species to the diet of Cape Gannets for two breeding seasons from October until February. Shown are sardine (*Sardinops sagax*), anchovy (*Engraulis encrasicolus*), saury (*Scorpaenopsis scorpaenoides*), hake (*Merluccius capensis* and *M. paradoxus*) and other species, in order of decreasing energetic content (Batchelor & Ross 1984)

	2003/04					2004/05				
	October	November	December	January	February	October	November	December	January	February
Sardine	54.7	58.9	18.1	21.4	24.1	30.8	5.7	10.6	10.5	21.0
Anchovy	11.4	29.8	53.3	21.8	0.0	8.5	4.2	3.0	6.7	18.0
Saury	2.7	0.5	21.1	53.3	75.7	18.5	19.3	64.0	59.0	49.6
Hake (offal)	30.7	8.4	4.3	0.0	0.0	33.3	35.7	21.0	10.8	4.9
Other	0.5	2.4	3.2	3.5	0.2	8.8	35.1	1.4	12.9	6.5

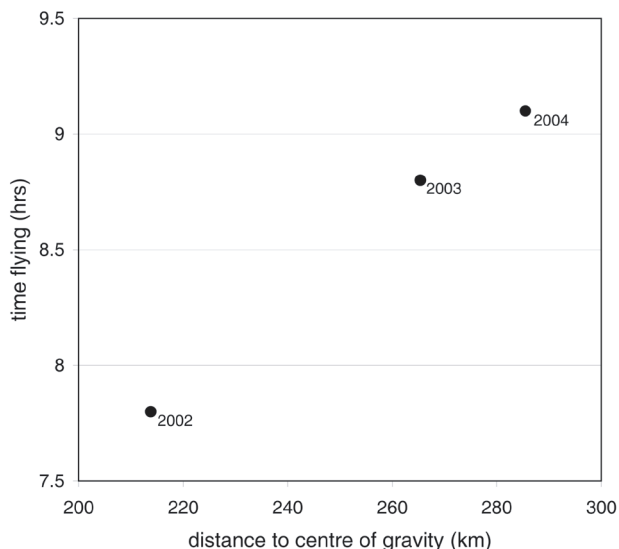


Figure 5: *Morus capensis*. Correlation between flying time (in hrs) and distance (in km) between Malgas Island and the centre of gravity of the sardine catches according to Van der Lingen et al. (2005). The dots represent the mean flying time for three seasons; 2002/03, 2003/04 and 2004/05. Data of 2002/03 from Grémillet et al. (2004)

Suryan et al. 2002), although seabirds may only switch their diet from certain preferred prey species once they reach below some level of abundance (Adams & Klages 1999; Suryan et al. 2002). The size and high energy content of sardines (8.59 kJg^{-1} wet mass, Batchelor & Ross 1984) make this fish most profitable for breeding Cape Gannets (Crawford & Dyer 1995; Adams & Klages 1999). Since 1997 the availability of both sardines and anchovies around the breeding colony at Malgas Island decreased due to eastward shifts in their distributions (van der Lingen et al. 2005). In 2003 the centre of gravity of sardine catches was near Gansbaai ($19^{\circ}30'E$), about 260 km flying distance from Malgas Island (van der Lingen et al. 2005). In 2004, this shifted eastwards to $19^{\circ}50'E$, a further 20 km flying distance in each direction. The eastward shift was reflected in the diet of the gannets; in 2003/2004 sardines and anchovies accounted for more than half of the diet, but their contribution decreased drastically the following season. Concomitantly hake and fish offal increased in the diet between the first and the second season. Hake offal has less than half the energy content of sardines (Batchelor & Ross 1984), therefore the amount of it that needs to be delivered to a chick is more than twice the mass of a chick's sardine requirements.

Intra-seasonal variability

Variation in foraging behaviour of chick-rearing gannets was evident within the two breeding seasons. In 2003/04 the duration of trips was 39.9% longer during the latter part of the breeding season than the first part; whereas in 2004/2005 longer trips were made in the first half of the season compared to the second half, with a 37% decrease in flying time between the two periods indicating a decrease in effort (Adams et al. 1991). Fluctuations in feeding trip duration would affect the provisioning rates and consequently growth of the chicks if parents were unable to compensate by the quality or quantity of the food brought back. While there is no data on quantity of food brought back, the association between foraging effort and chick growth indicates that gannets were not able to compensate. The period of higher foraging effort and faster chick growth during the 2004/2005

season was when sardines and anchovies still made a substantial contribution to the diet of the gannets. The decreased proportion of sardines and anchovies later that season suggests that these species had moved beyond the foraging range of breeding gannets at Malgas Island and the birds had to switch to lower quality food.

Previous studies showed that variation in chick growth was higher between days of measuring than between seasons (Shea & Ricklefs 1985 and 1996; Le Corre et al. 2003), suggesting short term effects of food availability on growth. It is to be expected that the chicks within a colony would, on average, be similarly affected by such short term fluctuations (Weimerskirch et al. 1997; Kitayski et al. 2000; Pinaud & Weimerskirch 2002). This expectation was realized in this study, as significant fluctuations in mean growth performance were evident within both seasons. The most striking feature of the chick growth patterns was the considerable variation between periods, particularly in 2004/2005 where mean growth rates fluctuated by orders of magnitude between consecutive periods. This was most likely associated with fluctuations in availability of the preferred prey species around the colony. Adams & Klages (1999) indicated that the availability of most profitable prey species, rather than prey availability *per se*, would affect switches in diet with consequences for foraging behaviour and chick growth. While sardines and anchovies were available throughout the 2003/04 breeding season, they decreased as the season progressed, with an associated decrease in growth performance of chicks. The reduced availability of these species in 2004/2005 relative to the previous breeding season was apparently associated with the wider variation in chick growth performance and the lower overall chick growth rate, measured in this season.

Inter-seasonal variability

During this study the distributions of the sardine and anchovy populations apparently shifted beyond the foraging range of the Malgas Island gannets. The birds increased their foraging effort, but were unable to sustain the amount of sardines and anchovies in their diet. In 2002/2003, the breeding season preceding this study, Grémillet et al. (2004) found that gannets from Malgas Island allocated less time to flying during their feeding trips (7.8 hrs) when compared to this study (8.8 and 9.1 hrs). The flying time and total distance of foraging trips appears to be linearly related to the distance between the colony and the centre of gravity of the sardine fisheries (van der Lingen et al. 2005, Fig. 5). Although the sample size is small, Fig. 5 suggests a proportional relationship between foraging effort and the mean location of the sardines. Foraging trip duration mainly depends on prey availability (Harris & Wanless 1997; Monaghan et al. 1989; Uttley et al. 1994), and the increase in foraging effort could therefore be seen as a response to the shift in prey distribution. Gannets were either trying to follow the sardines and anchovies or had to increase their foraging effort to obtain different, perhaps less abundant, species.

The decrease in sardine and anchovy in the diet was associated with a decrease in growth performance of the chicks (as in Adams et al. 1992). Gannets could in theory compensate for lower food quality by increasing the quantity brought back to the chick. Increasing the foraging effort does not necessarily improve the growth and/or survival of offspring (Takahashi et al. 2003). Parents are restricted by their optimal working capacity (Drent & Daan 1980; Fagerström et al. 1983) and therefore cannot increase the food load beyond a certain weight as flying is energetically expensive (Birt-Friesen et al. 1989; Adams et al. 1991). The fact that chick growth was lower by 28.6% in 2004/2005 following the de-

crease in availability of preferred prey species, sardines and anchovies, suggests that the scale of the decrease outweighed the extent to which parents could compensate with foraging effort. Consequently, breeding success was lower in the season with poor chick growth (36.6%) compared to the better season (54.5%, unpublished data).

Conclusion

Our data show that the long breeding season of Cape Gannets results in large fluctuations in foraging parameters of the adults and in growth of the chicks between consecutive weeks. Especially growth showed substantial fluctuations between weeks and therefore this parameter is not a very suitable predictor of breeding success if considered only over a short time frame (Suryan et al. 2002). The decreasing availability of sardines and anchovies during our research affected the foraging effort of breeding birds. Despite an increase in foraging effort between the two seasons, chick growth indicated that the parents could not compensate for the decreased availability of high quality food. The chicks were growing slower and had lower fledging rates, indicating the importance of high quality food for growing chicks.

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APPENDIX

Growth rates were calculated between each pair of successive measurements of mass. Thus, if mass at successive times t and u were m_t and m_u , the growth rate over this time period is $g = (\text{change in size})/(\text{time period}) = (m_u - m_t)/(u - t)$ and the mean of the pair of measurements is $a = (m_t + m_u)/2$. All pairs of values (a, g) were plotted, resulting in a growth rate against mass plot.

For a set of target masses the mean growth rate was estimated using a weighted regression. Weights for all pairs of observations were calculated (a, g) in such way that values close to the target mass had large weights and values farther away had increasingly smaller weights. If the target mass was m^* , then the weight w attached to observation (a, g) was $w = \exp(-((a - m^*)/\tilde{A})^2)$ where \tilde{A} was chosen to be 200, about 8% of the adult mass. The weight attached to observations 200g distant from the target mass is substantial (0.37), at 300g small (0.105), and at 400g tiny (0.018). Observations more than 400g distant from the target mass thus contribute negligible weights to the regression calculations. A weighted linear regression was fitted to predict growth rate from mass using these weights. The regression line, fitted by GenStat8 (GenStat Committee 2005), was used to predict the growth rate g^* at the target mass. Using this weighted approach, the estimated growth rate depends on observed growth rates in the neighbourhood of the target mass. By varying \tilde{A} , the extent of the influential neighbourhood can be modified. The value for \tilde{A} (200) was selected by visual inspection. However, the results do not depend critically on the choice of a particular value for \tilde{A} . Experimentation showed that if a chosen value was twice as large or half as small, the results would have been nearly identical.

An approximate standard deviation of mass was estimated for each target mass. The same weights used for the regression were used to estimate a weighted standard deviation s_{m^*} ; the formula $s_{m^*} = (1/n) \sum (w(g - g^*)^2)$ was used. An approximate coefficient of variation for each target mass was calculated as $CV^* = 100 \times (s_{m^*}/m^*)$. This coefficient of variation provides a measure of the variability of the growth rate for each target mass.

The estimated growth rates at each target mass were plotted, and the points were linked by interpolation. Likewise, approximate lower and upper confidence limits for the growth rates were plotted. A normal distribution was assumed, so that the lower and upper confidence limits were $g^* - 1.96 s_{m^*}$ and $g^* + 1.96 s_{m^*}$ respectively.

For each successive pair of measurements of a chick, a comparison was made between the observed growth rate and the expected growth rate in the interval between the two measurements. The expected growth rate was computed as the mean of the two measurements, and its approximate standard deviation calculated as described above. The standardized growth rate was then computed using the conventional approach to standardization – dividing the difference between the observed and expected growth rate by the standard deviation. In symbols, if the observed growth rate is g , the predicted growth rate is g^* and the estimated standard deviation at this growth rate is s^* , then the standardized growth rate z is defined to be $z = (g - g^*)/s^*$. For large samples, the overall mean of all z -values is asymptotically zero; negative values indicate growth rates below the mean and positive values, the opposite. The z -values can be interpreted as an index of the extent to which growth in the interval is above or below expected; through the mechanism of dividing by the standard deviation, the index is independent of the stage of growth.

If the scores are assumed to be normally distributed (which to a first approximation is probably reasonable), the magnitudes of z -values can be expected to be in keeping with the standard normal distribution; for example, approximately 95% of the z -values can be anticipated to lie between the values -1.96 and $+1.96$; less than 0.5% of the values can be anticipated to be smaller than -2.58 or larger than $+2.58$. All z -values above or below $+2.58$ and -2.58 respectively were screened for possible erroneous measurements or entries. Because the index is independent of growth stage, it becomes possible to investigate the effect of explanatory variables on growth rates.

