The commuting parent
Mullers, Ralf Hubertus Elisabeth

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CHAPTER 5

Foraging trips of breeding Cape gannets: their association with sex, diet, breeding success and colony status.

Ralf H.E. Mullers
René A. Navarro

Abstract
During four years 646 breeding Cape gannets (Morus capensis) at two breeding colonies were equipped with GPS-loggers to obtain insight in how foraging behaviour of gannets varied between colonies and whether it was predictive for the “health status” of these colonies. To study the association between foraging tracks and breeding success we also collected data on chick growth. Foraging behaviour of gannets from Malgas Island (South Africa) varied considerably during the breeding season; average trip durations could double between weeks. At Ichaboe Island (Namibia) foraging behaviour varied less, but the gannets made 2.3 h longer trips and had a larger foraging range than the gannets from Malgas. Gannets scavenging for fishery discards made shorter foraging trips than birds foraging for live prey (22.3 vs. 27.3 h respectively), during which they spent less time flying. Scavenging occurred more on Malgas. Chicks from Ichaboe were growing faster and had higher survival rates, possibly associated with the higher proportion of live prey in their diet. The fraction flown during foraging trips was positively associated with chick growth in the colony. Likely this relationship was mediated through diet, as gannets that made longer trips were more likely to return with (good quality) live prey. The fact that predation on chicks in the colony can be substantial and that overwinter mortality may vary a lot can explain why we could not confirm an earlier described relationship between parental foraging behaviour and colony status. The study of parental behaviour is important to explain chick growth, a component of colony health status, but inadequate to predict overall colony health status in Cape gannets.
INTRODUCTION

The status of populations is commonly assessed by establishing population size and/or growth rates, but these can only be generated and interpreted in retrospect (Krebs 2002). Understanding the processes that determine population growth, including adult survival and juvenile recruitment into the breeding colony, requires long term studies (Lebreton et al. 1992, Pradel et al. 1997). Parameters that can be collected in a short period and have predictive value for population dynamics might enhance the assessment of colony health status. Recently it has been suggested that behavioural data can be used as a proxy for colony health status and can be linked to population changes (Lewis et al. 2006, Grémillet et al. 2006, Petersen et al. 2008). Lewis and co-workers (2006) studied Cape gannets (Morus capensis) as a model species, a long-lived seabird in which foraging behaviour may well influence reproductive success and ultimately recruitment rates. Cape gannets from colonies decreasing in size worked harder, gained less energy during their foraging trips and had lower body condition than birds from growing colonies. The authors concluded from this work that ‘behavioural and state data can be used to identify important drivers of population change’. We have taken up this challenge and assessed whether foraging behaviour of Cape gannets is a predictor of chick growth, a parameter related to colony health status.

Variability in food supply potentially affects the foraging success of seabirds and thereby their breeding success and ultimately population numbers. Studies on the relation between parental foraging effort and chick growth or survival have shown that increased effort enhances reproductive output (Pugesek 1995, Wendeln & Becker 1999, but see Takahashi et al. 2003 for a negative result). Cape gannet pairs that made shorter foraging trips, and thus visited the nest more often, had chicks that grew faster and had higher survival (chapter 3). In this paper we will analyse how these differences relate to at-sea behaviour of foraging gannets.

Cape gannets breed in the Benguela upwelling-system off the southern African west coast, which is characterised by a high productivity sustaining large stocks of pelagic fish (Shannon & O’Toole 2003). The system is also highly dynamic; the intensity and location of the upwelling cells can vary considerably within years, affecting the short-term spatial distribution of fish (Shannon 1985). These short-term fluctuations overlay long-term spatial distribution patterns of the fish stock. Foraging seabirds need to adequately respond to these fluctuations and variation in foraging behaviour is expected (Suryan et al. 2002, Weimerskirch et al. 2005). Cape gannets in the Benguela mainly feed on anchovies (Engraulis encrasicolus) and sardines (Sardinops sagax) (Berutti et al. 1993, Adams & Klages 1999). The availability of these prey species has decreased considerably in recent years. Concomitantly population numbers of Cape gannets have also decreased (van der Lingen et al. 2005, Crawford
et al. 2007a). In Namibia numbers of breeding gannets in 2005 were reduced to only 5.1% of the numbers in 1956. Gannet numbers at the west coast of South Africa have decreased approximately 33% between 1997 and 2005 (Crawford et al. 2007a). Studies focussing on foraging behaviour of Cape gannets have so far been restricted to brief periods in the breeding season (Grémillet et al. 2004, Lewis et al. 2006, Pichegru et al. 2007). More detailed insight in the seasonal variation of foraging behaviour of breeding gannets is needed.

We studied foraging behaviour of Cape gannets during four breeding seasons by equipping gannets with GPS-loggers at two breeding colonies. At the same time we measured a large sample of chicks to determine growth in both colonies. We test the hypotheses that (1) variation within the breeding season in foraging behaviour is associated with chick growth and survival and (2) that such variation may be related to diet. We further investigate whether foraging behaviour may help to predict colony population dynamics.

METHODS

The Cape gannet is a monomorphic, long-lived seabird that feeds on different fish species by plunge-diving (Grémillet et al. 2004, Ropert-Coudert et al. 2004a). The entire world population breeds on six islands, three of which are located in Namibia and three in South Africa. Currently all five colonies that are situated at the west coast of southern Africa are decreasing in population numbers (Crawford et al. 2007a). Our data were collected during four breeding seasons (2003/04 to 2006/07) at Malgas Island (South Africa, 33°03’S 17°09’E) and during three breeding seasons (2004/05 to 2006/07) at Ichaboe Island (Namibia, 26°29’S 14°49’E).

Foraging behaviour of adults

GPS-loggers (Technosmart, Rome) recorded geographic positions of deployed birds. The loggers were sealed in two waterproof polyethylene bags, and weighed about 50 g or, approximately 2% of the adult body mass (mean 2531 g ± 194 in this study, n = 554). Birds at different stages of the breeding cycle were selected for carrying the loggers. We waited for gannets to return from a foraging trip. After the nest relief we caught the partner leaving the nest to forage with a hooked pole. In this way the chicks of focal birds remained attended by the partner (Lewis et al. 2004). The gannets were measured (length of the flattened wing chord to the nearest mm and bill length to the nearest 0.1 mm) and weighed (to the nearest 25 g). The logger was attached to the lower back and tail feathers with waterproof Tesa®-tape (Beiersdorf AG, Hamburg), which did not damage the feathers. The procedure took ca. 5 min, after which the birds were released near their nest site. Similar devices had no obvious
adverse effects on Cape gannet behaviour in previous studies (Grémillet et al. 2004, Lewis et al. 2006). The nest was monitored once per hour in daytime. When the parent with the logger returned it was recaptured and the logger removed. The birds were then released on their nests where they settled readily. Bill length, wing length and body mass (<1 kg to 5 g; >1 kg to 25 g) of the chick were measured to obtain an estimate of its age. Diet samples were collected from focal birds by inverting them over a bucket and collecting the regurgitated prey. The sexes could not be distinguished in the field. In two years (2005/06 and 2006/07) we collected some breast feathers of equipped birds and we determined their sex in retrospect through DNA analyses (see Fridolfsson & Ellegren 1999 for detailed methods). The overall sex ratio of sexed birds of which we obtained complete foraging tracks was 0.483 (97 males and 104 females). This ratio did not systematically vary between months (Multinominal regression: $\chi^2 = 2.8, P = 0.730$), so we were confident that among the gannets we equipped with GPS loggers there was no systematic over-representation of one sex that could have caused biased averages in foraging parameters between periods. For the analyses of foraging data we have pooled data of males and females and used the average of both sexes. This entails the implicit assumption that the sexes were also equally represented in the years without sexing (2003/04 and 2004/05).

In February 2007 we managed to collect only 10 complete tracks at Ichaboe Island. Due to changes in local food availability gannets left their chicks alone (chapter 3) and we refrained from further disturbances to the birds for fear of causing them to desert their offspring.

**Track analyses**

The GPS-loggers recorded the geographic positions (at ca. 10 m resolution) of each bird at 10 sec intervals. Before we could analyse the data we had to correct for the curved surface of the earth by converting the geographic coordinates of each GPS fix into a flat, two-dimensional surface through the Albers’ Equal Area Projection (Snyder 1982). From successive GPS positions of the birds ($p_t = $ position time $t$) we calculated the distance travelled ($D_t = $ distance between $p_{t-1}$ and $p_t$). From the distance and time between consecutive positions (usually 10 s intervals) we calculated travelling speed (km h$^{-1}$). During searching for prey gannets are expected to be less consistent in direction than during directional flight, and to have increased path sinuosity. Sinuosity at time $t$ was defined as the ratio between the distance flown (DF) between consecutive GPS positions and the straight line displacement (Di) between the start and end of the sinuosity window ($t \pm 2$). So, $DF_t = \Sigma \sqrt{(x_{t-1} - x_t)^2 + (y_{t-1} - y_t)^2}$ for $t = -1$ to $t = 2$, and $Di_t = \sqrt{(x_{t-2} - x_{t+2})^2 + (y_{t-2} - y_{t+2})^2}$, where $x$ & $y$ correspond with the projected coordinates (m) of longitude and latitude respectively.

By analysing the actual travelling speed and changes in speed and sinuosity, we could identify different behaviours of equipped gannets:
(1) Out-flight: from the departure from the colony until the sinuosity of the track was >3.3. This section is characterised by fast flight (usually over 40 km h⁻¹).

(2) Return-flight: segment of the track from last hunting activity back to the colony. The characteristics are similar to out-flights and it is identified by the algorithm by traversing the track in reverse order.

(3) Drifting on sea surface: characterised by speeds below 10 km h⁻¹. The night was part of this section. At night gannets sleep on the sea surface and drift along with ocean currents and prevailing winds (Ropert-Coudert et al. 2004b).

(4) Hunting (search flight): the remaining parts of the track, characterized by medium flight speeds (between 10-40 km h⁻¹) and larger values of sinuosity than out- or return-flights.

Foraging ranges were derived through concave polygon analyses with Ranges6 (Anatrace Ltd., Wareham, UK). Because gannets from Malgas Island would fly around Cape Point, we set the edge restriction to 0.1 in order to exclude land as part of the foraging range. This analysis does not take the density of the positions into account, but calculates the total area visited by birds.
Chick growth
To obtain an estimate of average chick growth for the colony and at different times during the breeding season, chicks were repeatedly measured at approximately weekly intervals and at several locations at the periphery of the colony. Because growth rates of chicks did not differ between the interior and the periphery of the colony (chapter 2) we minimised disturbance by sampling in the periphery. 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 described above for chicks of equipped birds). Measurements were started at the same time of the day and chicks were measured in the same sequence by only two persons (RHEM and RAN). The measurements continued until either the chick died or was completely feathered and ready to fledge. Chicks that hatched within the study sites were included in the measurements to obtain general data on the growth of young chicks throughout the breeding season. From the growth data we generated age-independent growth indices to compare growth between years and colonies (box 2.1).

In 2005/06 we caught and weighed chicks on both islands that were gathered at the edge of the colony and ready to fledge in order to get an estimate of average fledging weight.

Data analyses
In total 83.1% of the foraging tracks were complete (80.3% for Malgas and 88.4% for Ichaboe). The main reason for incomplete tracks was a lack of battery capacity to record the complete foraging trip. To calculate the average foraging parameters we used complete foraging tracks only (Malgas, \( n = 340 \); Ichaboe, \( n = 198 \)). For the spatial analyses we also included the incomplete tracks (Malgas, \( n = 422 \); Ichaboe, \( n = 224 \)).

Results are presented as mean ± standard deviation. The foraging data were In-transformed. After transformation trip duration and time spent drifting on the sea surface were not normally distributed and their associations with other variables were tested with non-parametric Kruskal-Wallis tests or Spearman correlations. The other variables were analysed using GLMs in which the potential explanatory effect of variables was tested using a backwards deletion method. Flying, hunting and drifting on the sea surface were also transformed into fractions of the total trip duration. The residuals of significant models were tested for normal distribution. Chick growth was analysed in multilevel models to control for repeated measurements of the same individual (individual and observation included as level). Multinomial regressions were used in models with sex or diet as dependent variables. Prey species were categorised in five groups; (1) anchovy and sardine, (2) saury (\textit{Scomberesox saurus}), (3) fishery discards (hakes \textit{Merluccius capensis} and \textit{M. paradoxus}), (4) other species, and (5) a mixture of live prey and fishery discards. Growth indices were
calculated using GenStat 8 and statistical analyses were done with MLwiN 2.02 (multilevel models) or SPSS 14.0 statistical package.

RESULTS

Sex-specific foraging behaviour
Table 5.1 provides the means and standard deviations of all foraging trips recorded for the sexes separately at Malgas (n = 136) and Ichaboe (n = 65) during 2005/06 and 2006/07. The table shows that female gannets made longer trips (28.7 h ± 13.4, n = 104) and covered more distance (409 km ± 220) during their trips than males (23.9 h ± 11.0 and 339 km ± 156 respectively, n = 97). Foraging trips of females from Malgas were on average 6.5 h (28.3%) longer than trips of males, covering an extra 95 km (22.0%). On Ichaboe the differences were smaller as female trip duration was only 1.1 h longer (4.0%), flying an extra 63 km (13.9%) compared to males. The difference in trip duration for birds from Malgas Island was mainly due to the extra 5 h that females spent drifting on the sea surface more than males (Table 5.1). The relative time allocation during foraging trips did not differ between the sexes on each island (Fig. 5.2). Despite differences in foraging trip duration and distance covered, foraging ranges did not differ between the sexes (One-way ANOVA: foraging range $F_{1,12} = 0.06$, $P = 0.812$, Table 5.2).

Table 5.1. Means ± SD of foraging parameters of Cape gannets per sex for A) Malgas and B) Ichaboe Island. Data are from 2005/06 and 2006/07. Results from GLM with sex and island as factors are shown at bottom of table. For trip duration and time drifting on the sea surface we show the Kruskal-Wallis test statistics ($\chi^2$) for the other variables the $F$-statistic. Significance is shown with * at the 0.05 level and with ** at the 0.01 level.
A body condition index (mass/wing length, see Lewis et al. 2006) was calculated for 2005/06 and 2006/07 and compared between the colonies and sexes. Cape gannets from Malgas were on average 152 g heavier, had longer wings and a higher body condition index (5.43 g mm\(^{-1}\) ± 0.38, \(n = 207\)) than birds from Ichaboe (5.18 g mm\(^{-1}\) ± 0.28, \(n = 135\)). Female gannets were 100 g heavier than males (females 2595 g ± 207, \(n = 113\); males 2495 g ± 183, \(n = 104\)), but the sexes did not differ in wing length. Consequently female body condition was 4% higher than that of males (GLMs: body mass: sex \(F_{1,214} = 18.9, P < 0.001\); island \(F_{1,214} = 41.1, P < 0.001\); wing length: sex n.s.; island \(F_{1,215} = 35.3, P < 0.001\); body condition: sex \(F_{1,214} = 21.0, P < 0.001\); island \(F_{1,214} = 26.4, P < 0.001\).

Table 5.2. Mean foraging ranges of Cape gannets per sex from Malgas and Ichaboe Island during two years. Sample sizes and ranges in km\(^2\) are shown.

<table>
<thead>
<tr>
<th>Island</th>
<th>Year</th>
<th>Sex</th>
<th>N</th>
<th>Foraging range (km(^2))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Malgas</td>
<td>2005/06</td>
<td>females</td>
<td>14</td>
<td>28 563</td>
</tr>
<tr>
<td></td>
<td></td>
<td>males</td>
<td>21</td>
<td>30 396</td>
</tr>
<tr>
<td></td>
<td>2006/07</td>
<td>females</td>
<td>55</td>
<td>38 088</td>
</tr>
<tr>
<td></td>
<td></td>
<td>males</td>
<td>46</td>
<td>40 912</td>
</tr>
<tr>
<td>Ichaboe</td>
<td>2005/06</td>
<td>females</td>
<td>30</td>
<td>39 067</td>
</tr>
<tr>
<td></td>
<td></td>
<td>males</td>
<td>26</td>
<td>34 551</td>
</tr>
<tr>
<td></td>
<td>2006/07</td>
<td>females</td>
<td>5</td>
<td>4 208</td>
</tr>
<tr>
<td></td>
<td></td>
<td>males</td>
<td>4</td>
<td>6 882</td>
</tr>
</tbody>
</table>

**Body condition**

A body condition index (mass/wing length, see Lewis et al. 2006) was calculated for 2005/06 and 2006/07 and compared between the colonies and sexes. Cape gannets from Malgas were on average 152 g heavier, had longer wings and a higher body condition index (5.43 g mm\(^{-1}\) ± 0.38, \(n = 207\)) than birds from Ichaboe (5.18 g mm\(^{-1}\) ± 0.28, \(n = 135\)). Female gannets were 100 g heavier than males (females 2595 g ± 207, \(n = 113\); males 2495 g ± 183, \(n = 104\)), but the sexes did not differ in wing length. Consequently female body condition was 4% higher than that of males (GLMs: body mass: sex \(F_{1,214} = 18.9, P < 0.001\); island \(F_{1,214} = 41.1, P < 0.001\); wing length: sex n.s.; island \(F_{1,215} = 35.3, P < 0.001\); body condition: sex \(F_{1,214} = 21.0, P < 0.001\); island \(F_{1,214} = 26.4, P < 0.001\).
**Inter- and intra-annual variation in foraging behaviour**

We averaged behavioural variables for each interval between consecutive measurements of chick mass and used these data to analyse the seasonal patterns in parental behaviour and the covariation between parental behaviour and chick growth for each island. The foraging variables (trip duration, total distance, time spent flying, hunting and drifting) were all positively correlated with each other, so we describe only the variation for trip duration in more detail for the seasonal variation.

Gannets from Ichaboe Island made longer trips during which they covered larger distances, flew more (23.5%) and spent more time hunting (32.3%) than birds from Malgas (Table 5.3). During foraging trips gannets from Malgas allocated a larger fraction of their time drifting on the sea surface than gannets from Ichaboe (GLM: island $F_{1,533} = 6.7, P = 0.010$; year $F_{3,533} = 21.4, P < 0.001$). The foraging ranges did not differ between the islands (One-way ANOVA: foraging range $F_{1,12} = 0.89, P = 0.364$, Table 5.2).

On Malgas Island average trip duration increased with 19.1% over four years, but did not vary significantly between years (Table 5.4A). Total distance increased with 14.9% over the same period, from 423 to 486 km. Time allocation during foraging trips changed after 2004/05; in 2005/06 and 2006/07 the percentage of time flying and time allocated to foraging activities were reduced and birds spent 35.7% more time drifting at the sea surface (Table 5.4A). Within years there was substantial variation in foraging behaviour on Malgas. To give an indication of the possible variation between weeks, we present average foraging variables for November 2005; in the first two weeks of the month gannets made foraging trips of 20.8 h, flying 349 km ($n = 32$), while in the last two weeks of that month gannets flew on average for 33.8 h, covering 631 km ($n = 20$) (Fig. 5.3A). Trip duration increased on average during the breeding season, except in 2004/05 when it decreased (GLM: year $F_{3,332} = 7.2, P < 0.001$; date $F_{1,332} = 12.0, P = 0.001$; year x date $F_{3,332} = 8.2, P < 0.001$).

**Table 5.3.** Means ± SD of foraging parameters of Cape gannets per island. Means are from four breeding season at Malgas Island (2003/04 until 2006/07) and three breeding seasons at Ichaboe Island (2004/05 until 2006/07). Results for GLM are shown, each model included island and year as factors. For trip duration and time drifting on the sea surface we show the Kruskal-Wallis test statistics ($\chi^2$) for the other variables the $F$-statistic. Significance is shown with * at the 0.05 level and with ** at the 0.01 level.

<table>
<thead>
<tr>
<th></th>
<th>Trip duration (h)</th>
<th>Total distance (km)</th>
<th>Time flying (h)</th>
<th>Time hunting (h)</th>
<th>Time drifting (h)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Malgas</td>
<td>24.6 ± 13.0</td>
<td>459.7 ± 240.7</td>
<td>8.1 ± 4.6</td>
<td>6.2 ± 3.8</td>
<td>16.5 ± 10.0</td>
</tr>
<tr>
<td>Ichaboe</td>
<td>26.8 ± 12.9</td>
<td>486.0 ± 210.9</td>
<td>10.0 ± 4.1</td>
<td>8.2 ± 4.0</td>
<td>16.9 ± 9.6</td>
</tr>
<tr>
<td>Sex</td>
<td>$\chi^2$ or $F$</td>
<td>$P$</td>
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<tr>
<td></td>
<td>4.6</td>
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<td>4.1</td>
<td>0.043 *</td>
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<tr>
<td></td>
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<td>$&lt; 0.001$ **</td>
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<td>0.743</td>
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</table>
Table 5.4. Means ± SD of foraging parameters of Cape gannets per year for A) Malgas and B) Ichaboe Island. Results from GLM per behaviour are shown below means. For trip duration and time drifting at Malgas we show the Kruskal-Wallis test statistics (\(\rho\) for date and \(\chi^2\) for year) for the other variables the \(F\)-statistic. For the year differences at Ichaboe we show the \(\chi^2\) from Kruskal-Wallis tests. Significance is shown with * at the 0.05 level and with ** at the 0.01 level.

<table>
<thead>
<tr>
<th></th>
<th>n</th>
<th>Trip duration (h)</th>
<th>Total distance (km)</th>
<th>Time flying (h)</th>
<th>Time hunting (h)</th>
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<td>A) Malgas</td>
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<tr>
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<td>7.1 ± 4.6</td>
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<tr>
<td>2005/06</td>
<td>52</td>
<td>25.8 ± 15.1</td>
<td>457.3 ± 275.3</td>
<td>7.3 ± 5.1</td>
<td>5.4 ± 3.8</td>
<td>18.5 ± 11.9</td>
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<td>2006/07</td>
<td>123</td>
<td>26.2 ± 12.6</td>
<td>485.8 ± 239.8</td>
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<td>24.6</td>
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<td>&lt; 0.001 **</td>
<td>&lt; 0.001 **</td>
<td>0.181</td>
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<td>22.1</td>
<td>14.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(\lambda)</td>
<td>0.403</td>
<td>&lt; 0.001 **</td>
<td>&lt; 0.001 **</td>
<td>&lt; 0.001 **</td>
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</table>

B) Ichaboe

<table>
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<tr>
<th></th>
<th>n</th>
<th>Trip duration (h)</th>
<th>Total distance (km)</th>
<th>Time flying (h)</th>
<th>Time hunting (h)</th>
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<td>485.1 ± 193.4</td>
<td>9.9 ± 3.9</td>
<td>8.1 ± 3.9</td>
<td>16.7 ± 9.3</td>
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<tr>
<td>2005/06</td>
<td>104</td>
<td>26.9 ± 13.5</td>
<td>486.7 ± 229.9</td>
<td>10.0 ± 4.3</td>
<td>8.5 ± 4.3</td>
<td>16.9 ± 9.9</td>
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<tr>
<td>2006/07</td>
<td>10</td>
<td>27.8 ± 12.1</td>
<td>486.8 ± 154.8</td>
<td>9.9 ± 3.2</td>
<td>7.3 ± 3.1</td>
<td>17.9 ± 9.2</td>
</tr>
<tr>
<td>(\chi^2)</td>
<td>0.02</td>
<td>0.07</td>
<td>0.08</td>
<td>0.75</td>
<td>0.11</td>
<td></td>
</tr>
<tr>
<td>(\lambda)</td>
<td>0.991</td>
<td>0.964</td>
<td>0.961</td>
<td>0.689</td>
<td>0.949</td>
<td></td>
</tr>
</tbody>
</table>

Cape gannets breeding on Ichaboe Island showed little variation in any of the foraging parameters between years (Table 5.4B). Birds made trips of approximately 27 h covering on average 486 km. During these trips they flew for about 10 h and drifted on average 17 h at the sea surface. Also within years we found no significant variation in trip duration, or any other aspect of foraging behaviour on Ichaboe (Fig. 5.3B).

**Foraging behaviour and diet choice**

Cape gannet diet did not differ between sexes or years, but varied between the colonies. Fishery discards occurred most in the diet of gannets from Malgas, followed by anchovy and sardine (Fig. 5.4). Gannets from Ichaboe mostly brought back saury...
or other live prey species (mainly snoek (*Thyrsites atun*) and horse mackerel (*Trachurus trachurus*)) (Multinomial regression: sex n.s.; year n.s.; island $\chi^2 = 11.2$, $P = 0.024$, Fig. 5.4). In general gannets that returned with live prey flew 145.2 km more (39.4%), spent 3.8 h more in flight (66.7%) and hunted for an extra 3.3 h (78.7%) compared to birds that scavenged behind trawlers (Table 5.5). If we look at the different foraging behaviours associated with diet per island, then gannets from Ichaboe returning with fishery discards flew 3 h more during their trips than birds from Malgas (8.0 h ± 2.0, $n = 9$; 5.0 h ± 1.9, $n = 28$, respectively). Also, gannets from Ichaboe spent 10.1 h (± 3.6, $n = 42$) flying when foraging for live prey, birds from Malgas 8.9 h (± 6.1, $n = 43$).

Figure 5.3. Average trip duration (h) (± 1 SE) of Cape gannet foraging trips per period of measurement of growth increment of the chicks for A) Malgas Island, and B) Ichaboe Island. Sample sizes for Malgas Island between 6 and 25 and for Ichaboe Island between 5 and 27 foraging trips per period.

Figure 5.4. Diet (in proportion of occurrence) of Cape gannets equipped with GPS loggers during the 2005/06 and 2006/07 breeding seasons. Sample sizes are 74 for Malgas Island and 56 for Ichaboe Island.
Chick growth and foraging behaviour

Chicks from Ichaboe showed faster growth rates than chicks from Malgas in each year (Fig. 5.5). Growth rates at Malgas decreased slightly over the four years. Chick growth on Ichaboe was reduced in 2006 compared to the two years before. Within each year chicks grew faster at the beginning of the breeding season than later (Multilevel model: island $\chi^2 = 92.6, P < 0.001$; year $\chi^2 = 16.1, P = 0.001$; date $\chi^2 = 33.0, P < 0.001$). In 2005/06 fledglings from Ichaboe were on average 305 g heavier than chicks from Malgas (Ichaboe 2930 g ± 275, $n = 107$; Malgas 2625 g ± 323, $n = 211$; One-Way ANOVA $F_{1,316} = 69.6, P < 0.001$). Some data on fledging success (percentage of nestlings fledged) of gannet chicks in both colonies are available. At Malgas Island fledging success in 2003/04 was 42% (Makhado et al. 2006) and at Ichaboe fledging success was 68% ($n = 53$ nests) in 2004/05 and 87% ($n = 23$) in 2005/06 (Ministry of Fisheries and Marine Resources, Namibia, unpublished data).

Table 5.5. Means ± SD of foraging parameters of Cape gannets, per diet category. Data are from 2005/06 and 2006/07. Results from GLM with sex, island and category as factors are shown at bottom of table. Significance is shown with * at the 0.05 level and with ** at the 0.01 level.

<table>
<thead>
<tr>
<th></th>
<th>n</th>
<th>Trip duration (h)</th>
<th>Total distance (km)</th>
<th>Time flying (h)</th>
<th>Time hunting (h)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Live prey</td>
<td>85</td>
<td>27.3 ± 12.0</td>
<td>514.6 ± 229.6</td>
<td>9.5 ± 5.0</td>
<td>7.5 ± 3.6</td>
</tr>
<tr>
<td>Fish offal</td>
<td>37</td>
<td>22.3 ± 9.9</td>
<td>369.2 ± 133.8</td>
<td>5.7 ± 2.3</td>
<td>4.2 ± 2.0</td>
</tr>
<tr>
<td>Mixed</td>
<td>8</td>
<td>27.6 ± 9.1</td>
<td>498.4 ± 185.4</td>
<td>8.9 ± 4.7</td>
<td>7.0 ± 3.3</td>
</tr>
<tr>
<td>Island</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>$F_{1,121}$</td>
<td>n.s.</td>
<td>6.1</td>
<td>11.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>n.s.</td>
<td>0.015 *</td>
<td>0.001 **</td>
</tr>
<tr>
<td>Prey category</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>$F_{2,122}$</td>
<td>2.6</td>
<td>6.6</td>
<td>7.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>0.078</td>
<td>0.002 **</td>
<td>0.001 **</td>
</tr>
</tbody>
</table>

**Chick growth and foraging behaviour**

Chicks from Ichaboe showed faster growth rates than chicks from Malgas in each year (Fig. 5.5). Growth rates at Malgas decreased slightly over the four years. Chick growth on Ichaboe was reduced in 2006 compared to the two years before. Within each year chicks grew faster at the beginning of the breeding season than later (Multilevel model: island $\chi^2 = 92.6, P < 0.001$; year $\chi^2 = 16.1, P = 0.001$; date $\chi^2 = 33.0, P < 0.001$). In 2005/06 fledglings from Ichaboe were on average 305 g heavier than chicks from Malgas (Ichaboe 2930 g ± 275, $n = 107$; Malgas 2625 g ± 323, $n = 211$; One-Way ANOVA $F_{1,316} = 69.6, P < 0.001$). Some data on fledging success (percentage of nestlings fledged) of gannet chicks in both colonies are available. At Malgas Island fledging success in 2003/04 was 42% (Makhado et al. 2006) and at Ichaboe fledging success was 68% ($n = 53$ nests) in 2004/05 and 87% ($n = 23$) in 2005/06 (Ministry of Fisheries and Marine Resources, Namibia, unpublished data).
We investigated whether average chick growth rates were associated with mean foraging parameters. Chick growth was positively correlated with the time spent flying during foraging trips, a relationship mainly due to differences between the two islands (Fig. 5.6). We found no correlation between any of the foraging variables and chick growth at the islands separately. In GLMs we tested separately the association between trip duration, distance and time spent flying with chick growth. In this analyses also time spent flying during foraging trips of adults was positively associated with chick growth, when corrected for island and date (GLM: island $F_{1,28} = 18.7$, $P < 0.001$; date $F_{1,28} = 5.8$, $P = 0.023$; time flying $F_{1,28} = 4.5$, $P = 0.043$). This pattern may be generated by differences in the use of fishery discards as food between islands and times of year.

**DISCUSSION**

In this study we showed that Cape gannets from Ichaboe Island (Namibia) had a lower body condition than gannets from Malgas (South Africa), but made longer foraging trips during which they flew more. Ichaboe gannets brought back more live prey from their foraging trips compared to birds from Malgas, which scavenged more behind fishing trawlers. During three consecutive breeding seasons the chicks were growing faster at Ichaboe and were heavier at fledging in 2005/06 compared to chicks from Malgas. Furthermore, chick growth was positively associated with the time spent flying during foraging trips, after correction for island and date.
Sex-specific foraging behaviour

Female Cape gannets made longer foraging trips and covered more distance than males, but during foraging trips both sexes allocated their time similarly between behaviours (Fig. 5.2). These results are consistent with our data on nest attendance (chapter 3) and demonstrate sex-specific foraging behaviour in a monomorphic species (Gray & Hamer 2001, Lewis et al. 2002). However, we found no differences in foraging ranges and in diet between the sexes and no difference in the amount of food brought back to the nest (females 542 g ± 135, n = 12; males 597 g ± 105, n = 12; L. Pichegru, unpublished data). Female gannets needed more time to bring back the same amount and kind of food as males, which may suggest a lower foraging efficiency, or differences in resource allocation between the sexes (Weimerskirch et al. 1997b). For example, females may have needed more self feeding to compensate energy loss for egg laying and incubation (Monaghan & Nager 1997).

In the related northern gannets (Morus bassanus) the sexes did not differ significantly in trip duration, but females made longer and deeper dives (Lewis et al. 2002). Here the ecological niche may differ between the sexes. To pursue this line for Cape gannets we will need detailed data on sex specific diving behaviour in this species.

Seasonal variability in foraging behaviour

The reduced availability of inshore shoaling pelagic fish around Malgas Island (van der Lingen et al. 2005) forced breeding Cape gannets to seek alternative prey. Early in the breeding season scavenging for fishery discards seemed to be an alternative. This involved shorter trips, less flying during the trips and smaller foraging ranges than birds bringing back live prey. Later in the breeding season saury move closer inshore and become available to gannets (Berruti 1988, Berruti et al. 1993), which was associated with an increase in the proportion of saury in gannet diet. This may explain the general pattern that foraging trip duration increased during the breeding seasons. In two years we collected GPS data during four consecutive months. In 2003/04, trip duration and distance covered increased during the breeding season, while in 2004/05 these parameters decreased, disproving the generality of the patterns at Malgas. Short-term fluctuations in the distribution patterns of prey fish are probably important to explain these deviations from the general pattern.

In contrast to Malgas the environment around Ichaboe Island was less variable, as judged from the small inter- and intra-annual variation in foraging behaviour of breeding gannets. Anchovies and sardines have been scarce in the Namibian waters since the late 1960s (Crawford 2007a). Live prey, mainly horse mackerel, was available...
as an alternative for anchovies and sardines throughout the breeding season. Unfortunately, no data on food availability in the Namibian waters is available. Nevertheless, judged from the longer foraging trips, overall food abundance was lower around Ichaboe (Boyd et al. 1994, Kitaysky et al. 2000, Suryan et al. 2002, Kowalczyk et al. 2006), but likely more predictable. Cape gannets from Ichaboe made longer foraging trips than birds from Malgas, despite a lower average body condition. The higher proportion of live prey in the diet of gannets from Ichaboe and its associated larger energetic and fat content (Batchelor & Ross 1984, FAO 1989) could facilitate higher levels of foraging effort (Weimerskirch et al. 2001).

**Foraging behaviour and chick growth**

Food availability during the breeding season is an important factor associated with chick growth and survival both directly, through amount and quality of the food (Batchelor & Ross 1984, Weimerskirch et al. 1997a), and indirectly, through behaviour of the parents (chapter 3). Chicks from Ichaboe had faster growth rates in three consecutive years and were heavier at fledging and had higher fledging rates than chicks from Malgas in 2005/06. If we assume that trip duration and time spent flying during foraging trips are reliable estimates of foraging effort (Lewis et al. 2006, Grémillet et al. 2006, Pichegru et al. 2007), then Cape gannets from Ichaboe worked harder than birds from Malgas. So overall, the larger foraging effort at Ichaboe was associated with faster chick growth. Despite the considerable intra-seasonal variation in both parental behaviour and chick growth, we found no direct correlations between these variables on each island. After correction for the variation explained by differences in conditions between the colonies and during the breeding season, chick growth was positively associated with the hours flying during foraging trips. In chapter 3 we showed that chick growth was negatively associated with the duration of foraging trips, due to lower provisioning rates. The relationship in this study is potentially mediated through diet. Gannets that spent more time flying, were more likely to forage for live prey, which is of better quality (energy content: sardine 8.59 kJ g⁻¹; anchovy 6.74 kJ g⁻¹; hake (fishery discards) 4.07 kJ g⁻¹, Batchelor & Ross 1984, FAO 1989) and enhances growth rates (Batchelor & Ross 1984, chapter 2). Gannet parents that feed on fishery discards compensate by bringing back more, but this was not enough to compensate for the reduced quality of the food (Pichegru et al. 2007).

**Foraging variables and population dynamics**

Lewis et al. (2006) investigated the association of Cape gannet’s behavioural and state data from 2003/04 with population changes before that time (between 1990 and 2002). They found that gannets from decreasing populations made longer foraging trips, gained less energy during those trips and had a lower body condition. Because we have new data on behaviour and more recent knowledge on population changes
over time, we can test whether Lewis’ relations still hold. To do so we relate the
behavioural data recorded by Lewis and ourselves with population changes between
2001/02 and 2005/06. This is important because it is a new test of the idea that
behavioural variables can be used as proxies for colony health status (e.g., Grémillet
et al. 2006).

We calculated population changes between 2001/02 and 2005/06 with updated
counts presented in Table 5.1 from Crawford et al. (2007a) to obtain an estimate of
population trends in 2003/04. All breeding gannets from Lambert’s Bay were chased
away by Cape fur seals (Arctocephalus pusillus pusillus) in 2005/06 (Crawford et al.
2007a), so population change there was calculated from 2001/02 to 2004/05. All five
breeding populations showed negative per capita growth rates between 2001/02 and
2005/06 (between -9.6% and -2.5%). The three largest colonies declined fastest,
producing a negative relationship between colony size and rate of population change
(slope = -1.01, $r^2 = 0.39$). This result is opposite to the result of Lewis et al. (2006)
as presented in their Fig. 1. In the new dataset Cape gannets from colonies that
declined fastest (2001/02-2005/06) made shorter trips, had larger daily energy gain
and a better body condition (Fig 5.7A + B). We therefore doubt that behavioural vari-
ables alone can be used as proxies for colony health status. For instance predation
plays a prominent role in determining breeding success and perhaps also in breeding
numbers (chapter 3). At Malgas predation pressure by kelp gulls (pers. obs.), great
white pelicans (Pelecanus onocrotalus) (de Ponte Machado 2007) and Cape fur seals
(Makhado et al. 2006) increased dramatically over the last few years, lowering the
number of fledglings. This lower overall number of fledglings may reduce the

Figure 5.7. A) Daily rate of energy gain (kJ d$^{-1}$) from Lewis et al. (2006) plotted against rate of
population change in Cape gannets between 2001 and 2005. B) Trip duration (h) from Lewis in
relation to rate of population change in Cape gannets between 2001 and 2005. The black dots in
5.7B are data from this study, but regression lines are only calculated from data of Lewis et al.
recruitment into the breeding colony, or even the settlement patterns, both affecting population dynamics. Mortality in Cape gannets is highest soon after fledging (Oatley et al. 1992) and associated with mass at fledging (Jarvis 1974). So, the better quality of the chicks from Ichaboe would potentially affect recruitment rates positively (Reid et al. 2003). Thus behavioural data on the foraging parents and the growth of their chicks do help to understand the potential health status of colonies; however a full demographic analysis is needed if we are to understand the recent changes in the breeding population of the Cape gannet.

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