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Foraging of a coastal seabird: flight patterns and movements of breeding Cape gannets *Morus capensis*

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Cape gannets *Morus capensis* are predatory seabirds in the coastal waters of southern Africa where they feed on commercially important fish species. Using a combination of intensive monitoring at nest sites, tracking of radio-tagged birds and diet sampling, we determined the foraging ranges and foraging areas used by breeding gannets, and whether links existed between the broad-scale spatial distribution of foraging birds and the distribution of prey or the predominant wind regime. A total of 270 Cape gannets dispersing to forage from Malgas Island, South Africa, were tagged over three consecutive breeding seasons. Modal durations of foraging flights were six or 24 hours, depending on whether birds returned on the same day they left or remained at sea overnight. Few birds remained continuously at sea over two consecutive nights. Non-radio-tagged birds more frequently undertook shorter foraging trips than radio-tagged birds, indicating a behavioural response to handling. Some 23% of radio-tagged gannets triangulated throughout a complete foraging trip foraged within a maximum of about 60km of Malgas Island, 44% foraged between about 60km and 120km of the island and the remaining 33% flew beyond 120km, travelling a total of at least 240km. Flight directions of gannets departing from the island were non-random in two of the three seasons. Return flight directions were non-random in all three seasons. Most foraging flights were to the south-west of the island, birds generally returning with the prevailing wind and from the same general direction in which they departed. Birds returning with saury *Scomberesox saurus* did so significantly more frequently from a west-south-west direction. Birds feeding on the other two prey species were equally likely to return from any direction. Under average conditions, the energy benefit associated with returning under load with a tailwind as opposed to a headwind was equivalent to 12% of the average stomach sample mass. The observed distribution of flights probably reflects the large area of suitable foraging habitat to the south and south-west of the island and the energetic advantages of returning with the prevailing wind.

Keywords: Cape gannet, feeding, *Morus capensis,* radiotelemetry, seabird, South Africa

Introduction

The foraging patterns of predatory seabirds should reflect, largely, the distribution, predictability and mobility of their prey (Wanless *et al.* 1998). The study of the nature of these predator-prey interactions in offshore and pelagic marine environments is challenging given the difficulty of sampling and making observations at the appropriate spatial and temporal scales. This problem is acute in volant seabirds that nest on land, but have the ability to fly rapidly, and feed on patchily distributed prey located at substantial distances from the breeding site.

Gannets (genus *Morus*) are one such genus of coastal seabirds, typical of temperate and cool-temperate waters of the northern Atlantic, southern Africa and Australia and New Zealand that feed on surface shoaling fish and squid (Nelson 1978). Substantial parts of their range overlap with waters exploited intensively by coastal-based commercial pelagic fisheries (Berruti and Colclough 1987, Montevecchi and Meyers 1995, Hamer *et al*. 2000, Bunce 2001). Studies of diets and prey harvests of northern gannets *Morus bassanus* and Cape gannets *M. capensis* at breeding sites in the North-West and South-East Atlantic Ocean have demonstrated correlations between relative proportions of specific prey species in their diet and interannual fluctuations in the abundance of this prey determined by fishery surveys and catches (Berruti and Colclough 1987, Montevecchi and Berruti 1991, Crawford and Dyer 1995, Montevecchi and Meyers 1995, Crawford 1999). The strengths of such correlations were sensitive to the spatial scale over which fishing and survey data are collated. The selection of the appropriate scales for analysis and their correct interpretation requires detailed knowledge of the foraging patterns and behaviour of seabirds. Such data are important for assessing their trophic interactions with commercial fisheries (Hamer *et al*. 2000) and understanding the causal links between prey abundance and seabird biology as observed at the nest. The demonstration of such direct links would enhance their use as indicators of change in populations of their marine prey that may provide supplementary input in fishery management models.

Cape gannets are colonial seabirds restricted to breeding on small offshore islands off the south-western and southern coasts of Africa (Nelson 1978, Crawford *et al*. 1983). The present study was conducted during the austral summer on gannets breeding at Malgas Island (33°02'S, 17°56'E), Saldanha Bay, South Africa (Figure 1). The island provides nesting sites for tens of thousands of breeding pairs of gannets (Crawford *et al*. 1983, Crawford 1999) and lies within the Benguela upwelling system. In common with the world's other four eastern boundary current systems, the Benguela system is characterised by equatorward surface flow, coastal upwelling, and high biological productivity, which supports a large biomass of a number of pelagic shoaling fish species (Crawford *et al.* 1987). Anchovy *Engraulis engrasicolus*, sardine *Sardinops sagax*, saury *Scomberesox saurus* and horse mackerel *Trachurus trachurus capensis* are important constituents of the diet of Cape gannets (Berruti *et al.* 1989). The proportions of these prey species in the diet of gannets have varied with environmental or fishing induced changes in their availability (Crawford 1999).

Developments in electronics and associated miniaturisation have allowed the development of transmitters and other remote-sensing devices small enough to be carried by free-flying individual seabirds (Wilson *et al*. 2002). This has made possible the study of the foraging behaviour of individual seabirds. In the present study, utilising favourable coastal topography, we used conventional VHF telemetry to examine some foraging variables of breeding Cape gannets. Radio telemetry has been used as a tool to elucidate the feeding behaviour of inshore feeding seabirds (Trivelpiece *et al.* 1986, Heath and Randall 1989, Wanless *et al*. 1990, 1991, 1998, Irons 1998, Litzow and Piatt 2003) and some offshore seabirds (Anderson and Ricklefs 1987, Harrison and Stoneburner 1981, Lewis *et al*. 2002). The relatively small unit cost of VHF transmitters allowed deployment of transmitters on a large number of birds.

The aims in this study were: (1) to define the spatial scale over which breeding Cape gannets, in particular, travel to feed, (2) to establish whether birds utilise specific foraging areas within their potential foraging area, and (3) if so, to test whether such patterns could be accounted for by distribution of preferred prey species or the prevailing wind regime.

Material and Methods

Telemetry

Transmitters were attached (see below) for a period of one to three days to a total of 270 birds attending chicks, with individual birds each being tracked for a complete foraging trip. In 1987/1988 and 1988/1989, radio-tracking sessions were conducted for a total of three to five days at monthly intervals from October to March. During 1989/1990, sessions were restricted to November and February, but lasted six and seven days respectively. Transmitters (150–152MHz) were housed in waterproof casings (50mm long × 15mm diameter) with a flexible antenna extended approximately 25cm long beyond the casing. The total package weighed a maximum of 20g, approximately 1% of adult gannet body mass. Transmitter housings were tied ventrally to the base of the shafts of two tail feathers using cotton carpet thread. Cyanoacrylate ester glue was applied to the knot to bond the thread to the feather shaft and to prevent slipping. The proximal section of the antenna was tied and glued to the feather shaft while the distal end was allowed to project beyond the tail. In this position, the transmitter housing was completely covered by the under-tail coverts.

Receiving equipment consisted of three 5-element and one 11-element vertically polarised paired Yagi antennae (null-peak system) mounted on a rotating mast and coupled to radio transceivers (Yaesu 50W 2m FM mobile). A compass rose, with zero set to true north, allowed direct reading of the bearings. The null-peak system has the ability to localise transmitters ±2° (Kenward 1987). At longer range, precision was reduced to ±5°. During 1987/1988, radio-tagged gannets were tracked from one receiving station located on Malgaskop, a small hill (113m) located on the mainland directly behind the island. Flight directions were obtained to and from Malgas Island only. During 1988/1989 and

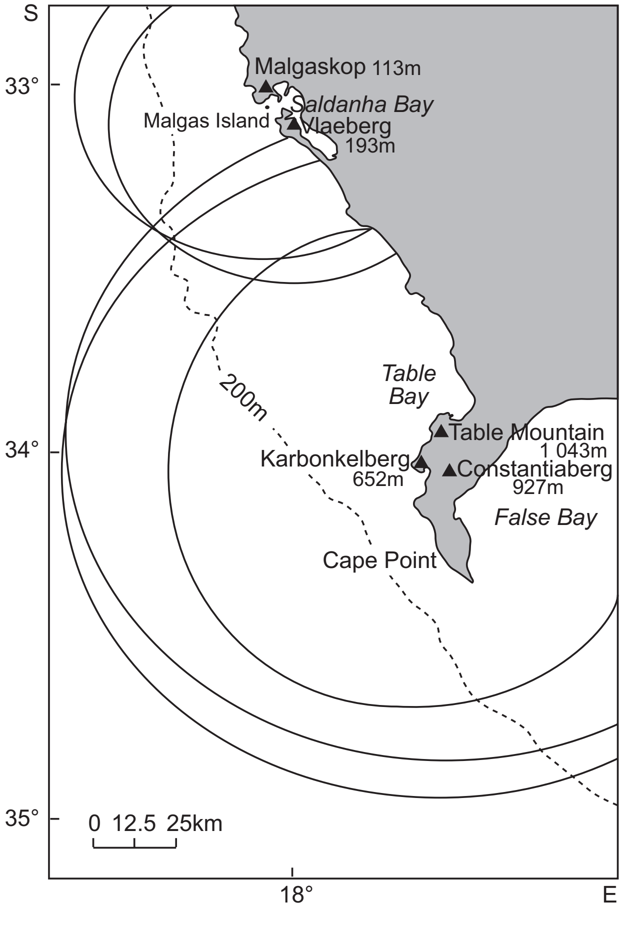

Figure 1: Map of the south-western Cape coast of South Africa showing location of Malgas Island and tracking stations. Concentric circles represent the maximum potential reception range of transmitters from tracking stations, indicated by filled triangles

1989/1990, birds were tracked from a combination of four of a possible five receiving stations, including Malgaskop (Figure 1). These stations were located on high points along the South-Western Cape coast (Figure 1) and allowed triangulation of bird positions at sea.

Handling procedure

At least one adult gannet is normally in attendance at a nest site throughout the chick-rearing period, with partners alternating foraging and attendance duties (Nelson 1978). Adult gannets were caught between 09:00 and 16:00, after having been recently relieved from attendance duties. After weighing, the transmitter was attached and the bird then released in vicinity of the nest site. Gannets generally left for sea within 30-minutes. Immediately following release of the adult, the chick was weighed. The marked nest was checked subsequently at 30-minute intervals from dawn to dusk until the radio-tagged adult returned. Chicks >500g were weighed at 3-h intervals (09:00, 12:00 and 15:00). On their return to the nest site, adult gannets were caught and induced to regurgitate their stomach contents, collected during foraging at sea. Regurgitation was induced by inverting the bird over a bucket and applying gentle pressure to the stomach. Once stomach contents had been recovered, radio transmitters were removed. A final weighing of the adult and chick allowed us to establish any additional mass gain. Adults can feed large chicks substantial amounts of food within a few minutes of arriving back at the nest. Therefore, this procedure allowed determination of foraging-trip duration and chick meal-size. We recognise that the total amount of food collected on a foraging trip was under-estimated on account of digestion and assimilation by the adult. However, the results are considered to be the best estimate of the foraging performance of gannets, against which tagged and control birds may be compared.

Flight directions and locations

Radio-tagged gannets were scanned from receiving stations at 15-minute intervals from dawn to dusk (05:00–20:00 in mid-summer). Gannets are visual predators and do not feed at night (NJA, unpublished data, see also Garthe *et al*. 1999). All departing birds could be tracked from Malgaskop for a minimum of 45 minutes. Ground speeds of flying gannets were determined by timing birds flying between a prominent rock and Malgas Island on a calm day (winds <5km h^{-1}) from Malgaskop. Based on this average flight speed, maximum detection distance from the island was about 60km (Figure 1). Birds remaining within this distance from Malgas Island could be tracked for the whole duration of their foraging trip from Malgaskop. Flight directions from the island were recorded as the last bearing before the signal was lost for outgoing birds and the first bearing recorded for incoming birds. Gannets were located at sea by triangulation of bearings to radio-tagged birds taken simultaneously from at least two receiving stations. Experimentation with a test transmitter indicated that we could detect transmitters from receiving stations on the Cape Peninsula (Table Mountain and Constantiaberg) at a range of 117km.

Because receiving stations for triangulating the position of gannets beyond the 60km radiotracking radius from Malgas Island were by necessity on high points to the south of Malgas Island, these extended foraging paths represent a biased sample of all possible tracks. We were unable to fix the positions of gannets travelling north of Saldanha Bay, birds travelling far offshore or far to the south of Constantiaberg.

Diet samples

Diet samples were analysed immediately after collection. Each sample was weighed and then sorted into its component fish species. Diet samples retrieved from Cape gannets were frequently well preserved and only rarely could prey species not be identified.

Weather data

Measurements of wind direction and speed are measured routinely at Port Control, Saldanha Bay, 4km from Malgas Island. Wind speed and direction is recorded continually. The day was divided into four 4-h periods and four hourly records were extracted for the days on which radio-tagged birds were monitored.

Transmitter and handling effects

Handling and attaching of devices on seabirds has the potential to affect both behaviour and foraging performance. These effects were tested by comparing foraging-trip durations and meal masses of radio-tagged birds with those of a control group of marked birds, the nests of which were checked regularly at 30-minute intervals. These birds were marked by dabbing dye on feathers of the chest and back with a paint brush on a 2m-long pole. Birds were not handled until captured for stomach sampling at the conclusion of a foraging excursion.

Statistical methods

Spatial distributions of incoming and outgoing flights were tested for randomness by comparing observed frequencies of flight directions grouped into seaside sectors of 20° against expected frequencies, assuming that gannets utilise each sector randomly. Cells closest to the shoreline were grouped to avoid zero values in some months. The G statistic for the log-likelihood ratio goodness-of-fit test for expected and observed distributions was computed. Significance levels were set at $p < 0.05$.

The Benguela upwelling system is a complex and dynamic region (Shannon 1985) and fish survey data indicate substantial changes in mesoscale fish distribution (100–1 000km) between seasons and between years (Hampton 1987). Accordingly, we tested for consistent flight patterns at the smallest temporal scale compatible with an appropriate sample size in each cell. Pooling data over seasonal and interannual scales may reduce the chance of detecting patterns in foraging. We tested for significant differences among observed flight direction frequency distributions for six defined seasons (early summer [October–December] and late summer [January–March]) for 1987/1988, 1988/1989 and 1989/1990 using the χ^2 test. By examining the adjusted standardised deviates calculated for each cell in the contingency table (Everitt 1977), it was possible to identify for each 20° flight sector where observed and expected values differed significantly. Positive values indicate deviates greater than expected, negative values indicate deviates lower than expected, adjusted deviates >3.291 are significantly different from expected values at $p < 0.001$ (Everitt 1977). The significant p value was set conservatively to account for repeated comparisons of the same dataset.

Under the assumption that potential prey species showed consistent mesoscale patterns of distribution, a similar approach was used to test for the effects of prey type on flight direction on the combined dataset.

In the absence of other factors, if wind direction affects flight patterns of Cape gannets, it was predicted that gannets on their outward flights from Malgas Island would head at an angle to the wind that optimises flight efficiency. However, given that other factors may influence flight directions, such wind effects may only be significant at high wind speeds. In addition, it was predicted that the deviation between outgoing flight direction and prevailing wind direction would decrease significantly with increasing wind speed. These predictions were tested by examining the correlation between both the deviation in flight directions and the outgoing flight direction, and the wind direction at time of departure. This analysis was performed at two different wind speed categories (> or < 20km h^{-1}). Patterns in the variances in direction of outgoing flight directions — wind direction against wind speed — were examined (one-tailed variance ratio F-test, Zar 1984).

Significant differences in the distribution of foraging-trip durations (log-likelihood ratio test) and meal mass (nonparametric, unpaired two sample analysis) were tested between control birds and birds handled for attachment of transmitters. Stomach sample mass was not corrected for digestion. Accordingly, the data were separated into samples recovered from birds (1) the same day that they departed from the colony and (2) that remained away overnight.

Results

Both the control and handled groups showed a trimodal distribution of foraging trips for birds returning from foraging on the same day they departed, those remaining at sea overnight before returning or those occasionally remaining at sea for two nights. The frequency distributions of foraging-trip durations of handled and control birds were significantly different ($\chi^2 = 625.4$, df = 11, $p < 0.0001$, Figure 2). Control birds more frequently went on shorter trips than the handled birds.

In contrast, there were no significant differences in the meal mass between tagged and non-tagged birds that returned within a day (Z = –1.67561, p = 0.0938) or between these two groups of birds when they stayed away overnight (Z = –1.168 1, p = 0.2427).

The directions of flight combined for all three years showed a non-random distribution. Birds generally departed and returned on a constant heading, concentrating in the south-western sector. When examined on an annual basis, the spatial distribution of flights of departing birds was non-random in the breeding seasons of 1987/1988 and 1989/1990, but not significantly different from random in 1988/1989 (Figure 3, Table 1). The frequency distribution of arrival flights was non-random in all seasons sampled.

Departure flights in 1989/1990 and late summer 1988/1989 were dominated by flights between 191° and 210°;

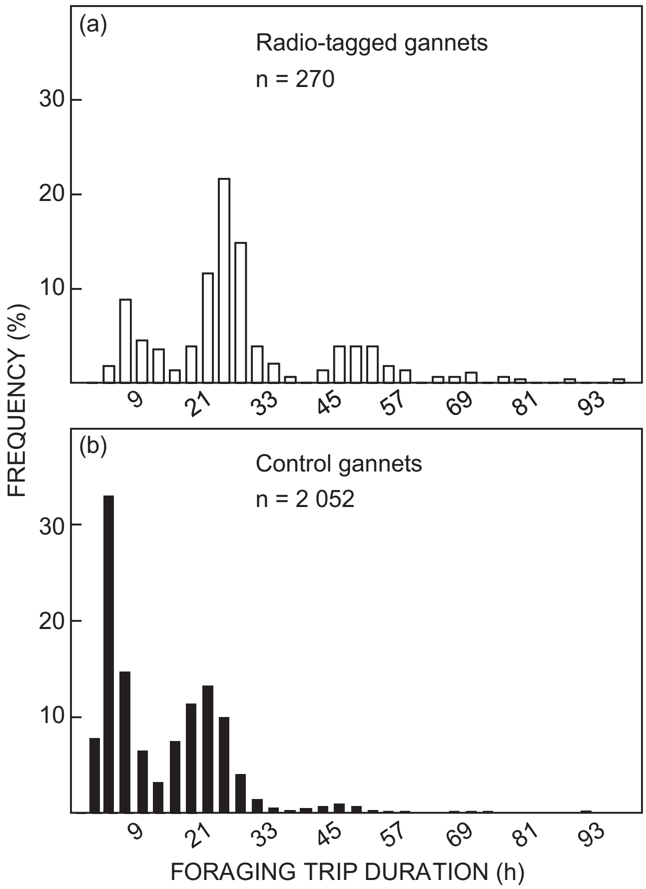

Figure 2: Foraging trip durations of (a) radio-tagged and (b) control gannets

Table 1: Results of log-likelihood ratio goodness-of-fit test to assess whether the spatial distributions of flights to and from Malgas Island were different from random

Breeding season	G Statistic	df	p
	Outgoing flights		
All years	14.96	5	< 0.05
1987/88	31.07	5	< 0.05
1988/89	7.53	5	ns
1989/90	18.14	5	< 0.05
	Incoming flights		
All years	49.19	5	< 0.005
1987/88	30.88	5	< 0.05
1988/89	12.35	5	< 0.05
1989/90	13.96	5	< 0.05

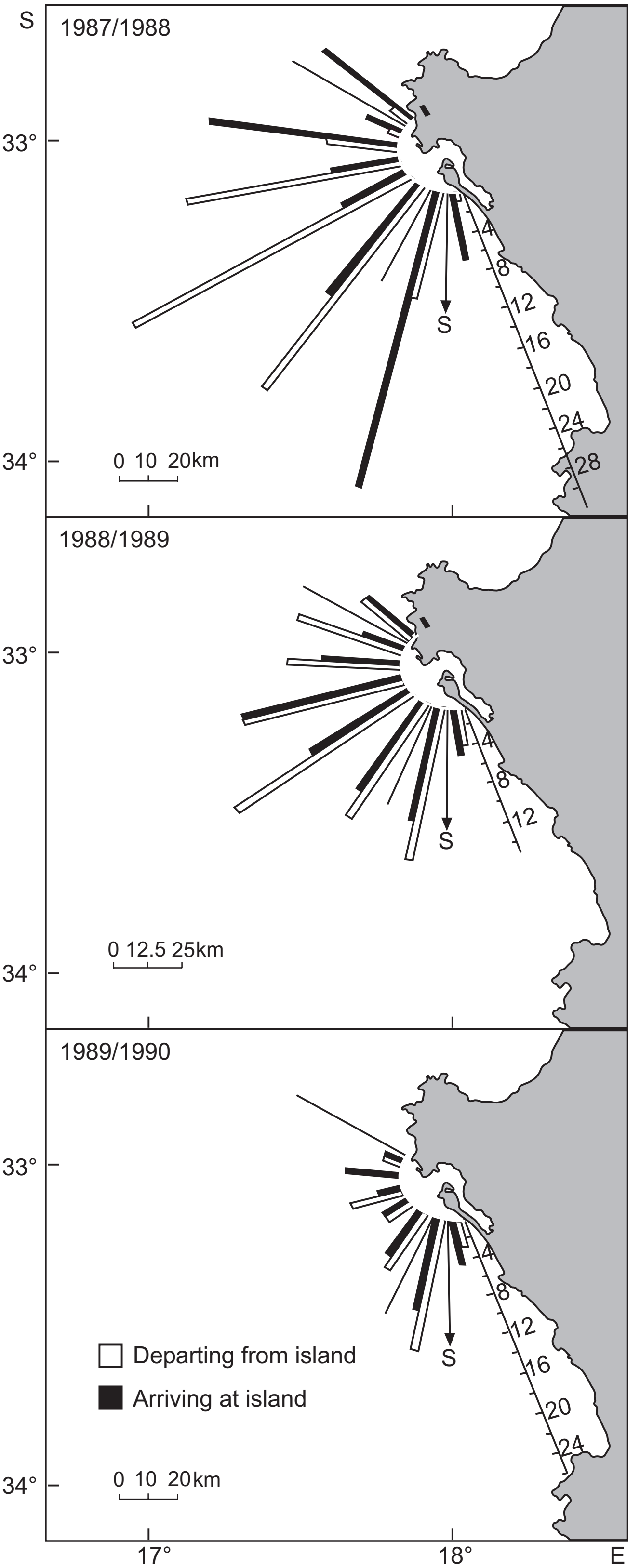

Figure 3: Flight directions of gannets departing and arriving at Malgas Island lumped in 20° sectors for three consecutive breeding seasons, 1987/1988, 1988/1989 and 1989/1990. Frequency of a particular flight direction is indicated by length of bars.

flights during early summer 1988/1989 and 1987/1988 were dominated by directions from about 251–270°. During late summer 1987/1988, flights were concentrated in the region 211–250°.

The χ^2 test for seasonal differences among flight patterns was restricted to 1987/1988 and 1988/1989. Inclusion of the 1989/90 data resulted in violation of the test requirement that <20% of the cells in the contingency table of expected frequency occurrence should be <5 and no cell should have an expected frequency of <1. Flight direction frequency distributions varied significantly between seasons (χ^2 = 59.2, df = 15, p < 0.0001). Adjusted residuals calculated for each contingency table cell indicated gannets flew out more frequently than expected in the 231–250° sector and 211–230° sector in early summer 1987/1988 and late summer 1987/1988 respectively (Table 2). In late summer 1988/1989, birds flew out more frequently than expected in the <190° sector.

Although only a relatively small proportion of the variance was explained, the direction of outgoing flights of individual birds was correlated with the direction of their incoming flights (r^2 = 0.264, n = 159, p < 0.001). This indicates that birds showed a tendency to return on the reciprocal bearing to the direction in which they departed.

The maximum distance radio-tagged birds travelled from the island in a single foraging trip of 6–24h was highly variable (<10km – >120km, Figure 4). Of all birds tracked in the reception area (see Figure 1), 23% remained within receiving distance of Malgaskop for the duration of the foraging trip (within about 60km of the island), 44% reached their maximum range within the area north of a line due west of Constantiaberg to the southern limit of the receiving range from Malgaskop (60–120km from Malgas Island), and 33% of birds travelled to areas south of Constantiaberg (>120km from Malgas Island, Figures 4, 5). At least one bird moved into False Bay to forage. Gannets avoided the inshore area 10km from the coast between Saldanha Bay and Table Bay. Distances covered by birds whose position was fixed within 30 minutes of dusk and one hour of dawn were generally short and indicated that there was little or no movement at night. There was no significant correlation between the duration of a foraging trip and foraging range (p > 0.05). Average flight speed of Cape gannets was 63km h^{-1} (range: 56–67km h^{-1}) indicating that feeding areas were potentially nearly all within two hours flying time of the breeding island. Given the inherent bias in the data because of the limited tracking range, these data should be interpreted with caution.

In all, 57% of all winds recorded at Malgas Island during the study period were from a south-westerly to southerly direction. The strongest winds were also recorded blowing from this direction (Figure 6).

Examination of the frequency at which different sectors were used by returning birds that fed on different prey indicated that those eating saury returned significantly more frequently in the 231–250° sector (p < 0.001, adjusted residual = 4, Figure 7).

There was some suggestion that wind influenced gannet flights, because variability in direction of departure flights in relation to prevailing wind direction was significantly lower at high winds speeds (>20km h^{-1}) than at low wind speeds (F = 2.156, p < 0.05). However, there was no significant correlation between flight direction of departing gannets and wind direction when all data were considered at wind speeds >20km h^{-1} ($p > 0.05$). It is concluded that birds did not select a specific heading relative to wind direction.

Discussion

Breeding Cape gannets showed a behavioural response to handling for the attachment of transmitters. The birds under study increased the average duration away from the nest compared to control birds (see also Adams and Klages 1999). Northern gannets handled as part of a study of activity-specific metabolic rates showed similar adverse responses to handling (Birt-Friesen *et al.* 1989), with manipulated birds spending less time at the nest than control birds. However, northern gannets fitted with platform terminal transmitters, in a similarly short handling procedure as the present study, showed no difference in foraging-trip durations from those of control birds in a study examining foraging ranges and feeding locations in the North Sea (Hamer *et al*. 2000). The magnitude of such effects in coastal seabirds appears case, species and breeding-status dependent. For example, alcids feeding chicks were less sensitive to such disturbance than pre-breeding or incubating birds (Wanless *et al.* 1985) and the frequency of chick feeding by two species of auks, *Uria aalge* and *Alca torda,* were adversely but differentially affected (Wanless *et al.* 1985, 1988, 1989). On the other hand, attendance behaviours of the black-legged kittiwake *Rissa triactyla* were unaffected by handling (Irons 1998).

In addition to the behavioural effects associated with handling (see above), the devices themselves, particularly if 2.5% or more of body mass, may affect locomotory efficiency and cost by adding mass and increasing drag (Gessaman and Nagy 1988, Obrecht *et al.* 1988). However, it is suggested that the tail-mounted transmitters, weighing a maximum of 1% of body mass and completely covered by the undertail coverts, would have a negligible effect on the ability of gannets to catch prey. Lack of any significant differences in meal mass of the tagged and control Cape gannets supports this conclusion. Similarly, internal and small external temperature loggers attached to the legs of northern gannets did not detrimentally affect their foraging efficiency (Garthe *et al*. 1999).

In summary, it is considered that the longer periods of absence of radio-tagged Cape gannets from nests reflect a direct behavioural response to handling rather than inefficient prey capture.

In all, 67% of all birds tracked at sea remained north of Constantiaberg, within about 120km of their nests on Malgas Island. The specific concentration of birds recorded foraging a maximum of 91–110km from Malgas Island may be partly an artefact of the two southern receiving stations being located on the coast directly opposite this feeding area. However, these measurements are consistent with at-sea observations of Cape gannets of unknown status marked with coloured dye at Malgas Island and a recent study using GPS tracking. These indicated a longshore foraging range of 200km during summer (Berruti 1987) and a maximum

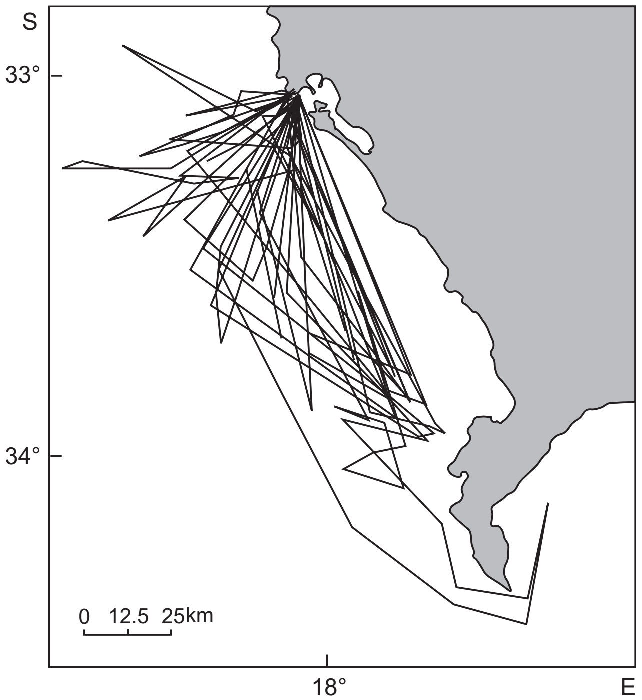

Figure 4: Flight paths and foraging ranges of gannets tracked at intervals throughout a complete foraging excursion

Table 2: Adjusted residuals of chi-squared ratio goodness-of-fit test for outgoing flight directions over four consecutive partial breeding seasons. All directions north of due west and <190° were grouped to increase sample size in individual cells. The remaining flights were grouped in 20° sectors. Positive values indicate deviates greater than expected, negative values indicate deviates lower than expected. Critical values are from the Student's t-distribution with infinite degrees of freedom

Flight direction sector	1987/88 Early summer	1987/88 Late summer	1988/89 Early summer	1988/89 Late summer
<190°	–2.3	–1.6	0.2	3.9*
191–210°	–1.7	0.8	0.8	1.4
211–230°	–1.4	3.6*	–2	– 0.6
231–250°	4.1*	–2.0	0	– 1.4
251–270°	0.2	1.5	0.5	–2.5
>270°	0.5	–2.6	2.8	– 0.5

* Adjusted deviates > ±3.291 are significantly different from expected values at $p < 0.001$

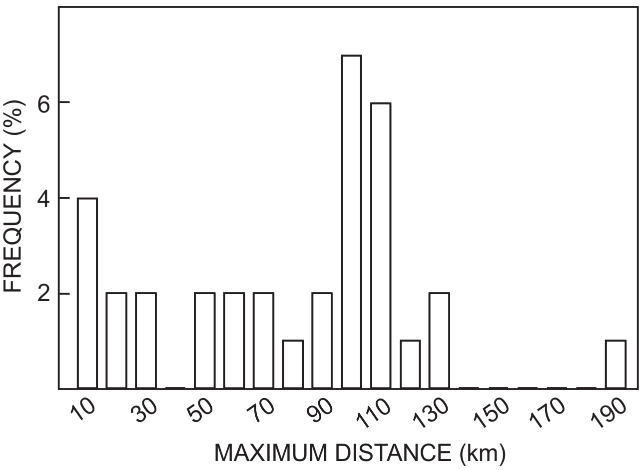

Figure 5: Maximum distances attained by individual gannets from Malgas Island during foraging trips for which radio location data were available throughout a complete foraging trip

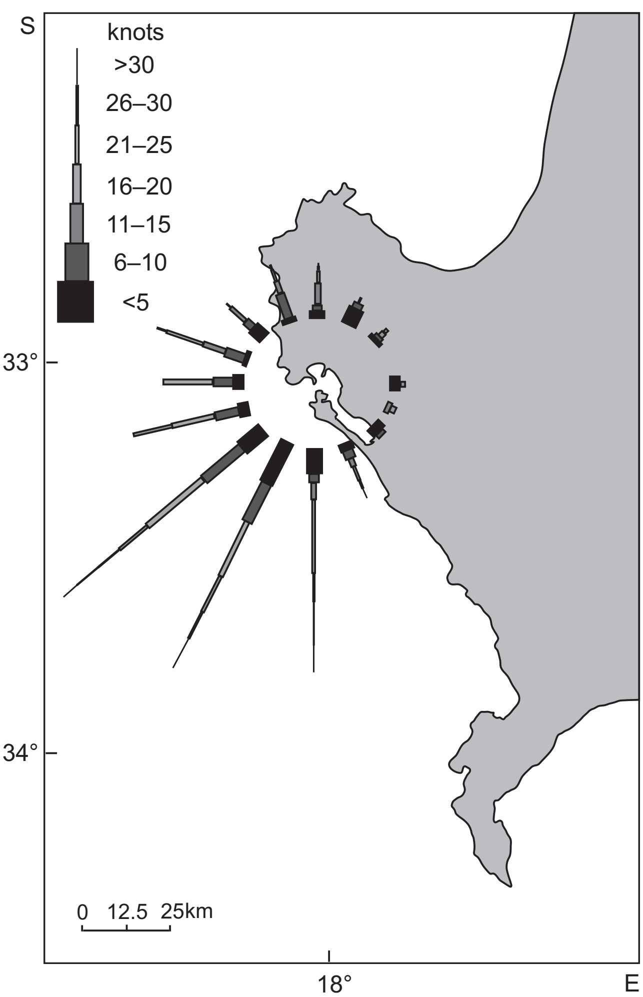

Figure 6: Relative frequency of occurrence of wind direction and strength recorded at Malgas Island during days that birds were tracked by radiotelemetry. Length of bar represents frequency with which a particular wind speed was recorded

distance of 104km (Grémillet *et al.* 2004) respectively; although the later study, not restricted by the topographic constraints of VHF telemetry, indicated that some individual birds travelled considerably farther than this (Grémillet *et al.* 2004). The range in travelling distances recorded for Cape gannets is similar to earlier estimates for northern (Kirkham *et al*. 1985, Tasker *et al*. 1985) and Australasian gannet *M. serrator* (Wingham 1985). Mean maximum foraging range of northern gannets estimated from activity budgets was 128km for birds that averaged 13h away from nests on Hermaness, Shetland, UK (Garthe *et al.* 1999). All these measurements and estimates reflect the coastal feeding habits of gannets and foraging trips that are

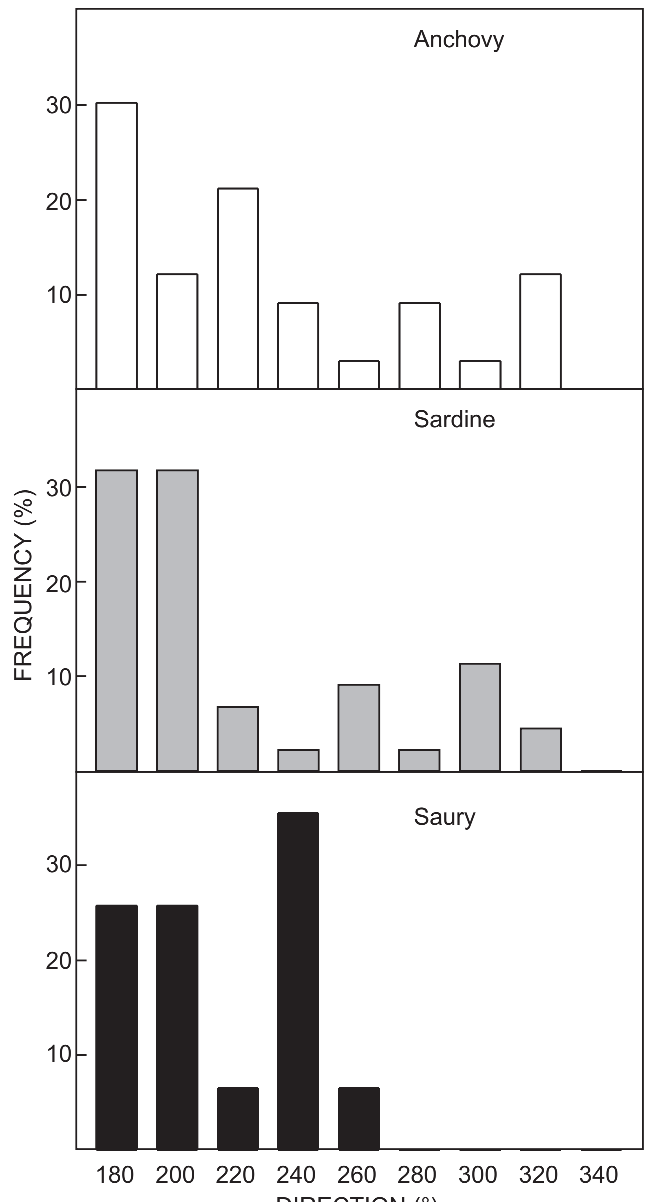

Figure 7: Numbers of Cape gannets returning to Malgas Island with single species prey loads in relation to arrival direction

restricted usually to 36h or less. These values are somewhat less than earlier estimates of foraging ranges of Cape gannets of 270–360km based on distribution at sea and recovery of banded adults (Rand 1959) and of 470km based on parental nest attendance and estimated flight speed (Jarvis 1971). They are also less than the maximum range of 540km and the mean distance to farthest point on any one trip of 232km measured for northern gannets using satellite telemetery (Hamer *et al*. 2000). Significantly, foraging trips of these birds nesting on Bass Rock, South-East Scotland, ranged from 13h to 84h (Hamer *et al*. 2000).

The foraging range of gannets on individual foraging excursions from Malgas Island over the duration of the study did not correlate with trip duration. This observation is consistent with data that show gannets attending chicks may spend <50% of their time at sea actually flying (Adams and Klages 1999, Garthe *et al*. 1999), providing them with considerable flexibility to respond to variation in food availability among foraging trips and still maintain a consistent food delivery rate to chicks (Burger and Piatt 1990, Adams and Klages 1999). It is also consistent with the trimodal distribution of foraging-trip durations coupled with little movement at night. The present result is in marked contrast to Hamer *et al.* (2000), and that of Grémillet *et al*. (2004), who demonstrated that the trip duration of northern gannets and Cape gannets explained most of the variation in distance travelled. This may reflect marked differences in the spatial and temporal predictability of prey between and within the two marine systems, although demonstrated disturbance effects and the bias owing to the limited tracking range require some caution in interpretation.

Much of the patchiness in seabird distribution in the southern Benguela upwelling system determined from transects carried out at sea, which is probably related to prey patchiness, was at scales of 0.3–10km (Schneider and Duffy 1985). This is at a scale too small to be investigated using VHF or indeed current satellite telemetry technology. Non-random distribution of foraging flights of seabirds reflecting movement at larger spatial scales has been considered to reflect the location of favoured feeding areas with respect to nesting sites (Harrison and Stoneburner 1981, Anderson and Ricklefs 1987, Hamer *et al*. 2000). Such feeding areas may represent spatially predictable mesoscale (10–100km wide) oceanographic features (see Hunt and Schneider 1987), which are presumed to concentrate primary production and seabird prey (Heath and Randall 1989, Jouventin *et al.* 1994). In spite of a generally consistent pattern of dispersal maintained over a number of seasons, we are unaware of any bathymetric features in the southern Benguela system (Shannon 1985) that concentrate seabird prey in such a spatially and temporally predictable way. Enhanced primary production is associated with well-developed and spatially predictable upwelling cells located off the Cape Peninsula and Cape Columbine (Shannon 1985), 120km to the south and 30km to the north respectively of the study site. A close association between these sources of enhanced primary production and abundance of seabird prey species at equivalent spatial scales has not been demonstrated.

At a larger, regional scale (macroscale: 100–1 000km; Hunt and Schneider 1987), populations of adult sardine and anchovy around South Africa are generally restricted to cold coastal waters over the continental shelf (Armstrong *et al*. 1987, Crawford *et al*. 1987, Hampton 1987). Therefore, the generally south-west mainly longshore movement of gannets may reflect, partly, the location of the shelf (Figure 1). Birds flying west would soon encounter the edge of the shelf break (depth >200m) and the limit of the distribution of sardine and anchovy. Of note is the more westerly distribution of the flight directions of gannets returning with saury. In contrast to anchovy and sardine, saury are associated with oceanic water and thermal fronts (Dudley *et al*. 1985, Berruti 1988). The continental shelf break and associated oceanic water is in closest proximity to foraging gannets due west of Malgas Island (Figure 1).

Although wind speed and direction has a major influence on large-scale foraging movements of some pelagic seabirds (Jouventin and Weimerskirch 1990, Weimerskirch *et al*. 2000), there was little evidence of such influences for Cape gannets departing from Malgas Island (but see Grémillet *et al.* 2004). Nevertheless, on account of the direction and persistence of the prevailing wind, gannets often left quartering into the wind and food-laden gannets

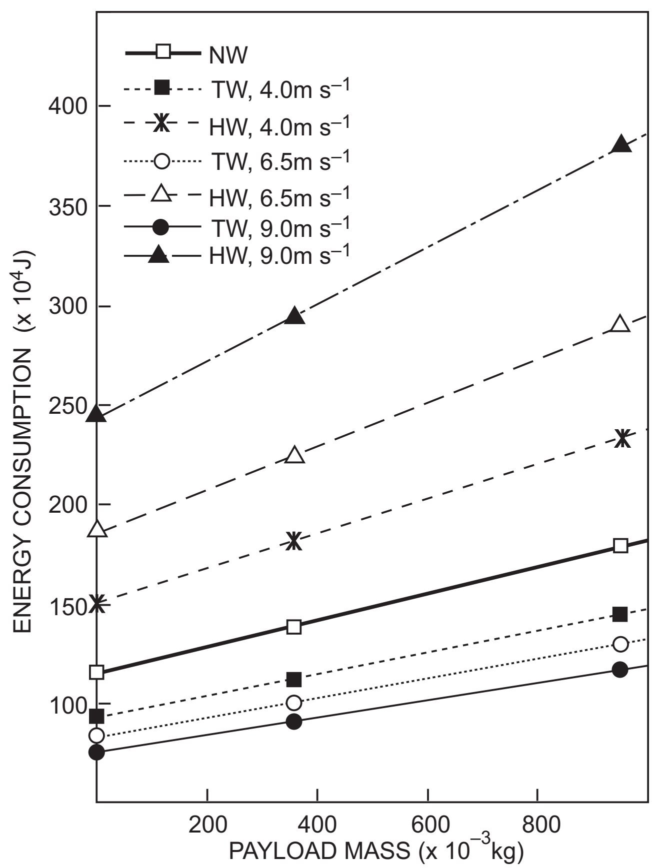

Figure 8: Total energy requirements (calculated from Pennycuick 1989) for a 100km flight by a Cape gannet (mass = 2.63kg, wing span = 1.73m, flight speed = 17.2m s^{-1}) carrying payloads ranging from zero, through mean accumulated mass (0.358kg) to the maximum recorded (0.95kg) under various wind conditions (NW: no wind, TW: tailwind, HW: headwind). The most frequently recorded wind speed at Malgas Island was 6.5m s^{-1}

returning to the colony frequently did so while flying with a tail wind. The coincident flight and wind pattern will confer some energetic benefits to food-laden gannets. Based on programmes developed by Pennycuick (1989), we used the approach of Schaffner (1990), and quantified the energy savings inherent in the observed flight patterns in relation to prevailing wind conditions. Variations in the wind strength and payload have little effect on the total energy costs of a 100km flight when birds are flying downwind (Figure 8). However, with headwinds of the order experienced at Malgas Island during the summer, energy costs increased substantially, particularly at high loads equivalent to the maximum recorded for gannets (Figure 8). For a payload equivalent to the mean mass accumulated over a foraging trip (0.358kg), the total energy cost of a 100km flight with and against the wind of the most frequently recorded speed (6.5m s^{-1}) is 9.98×10^5kJ and 22.4×10^5kJ respectively. However, because birds feeding chicks are central-place foragers and must return to the nest, it is more appropriate to examine differences in energy costs of a 200km round-trip. The difference between birds returning under load with a head wind versus the opposite condition is 2.03×10^5kJ (30.7×10^5–28.7×10^5kJ). Assuming a metabolisable energy content of 4.89kJ g^{-1} wet mass for gannet prey (Adams *et al.* 1991), this difference is equivalent to 41g of fish. Summed over the duration of a breeding season, energy saving accrued by feeding upwind of nesting sites may be considerable. There are very few suitable breeding sites off the South African coast and constraints other than the local wind regime may be more critical in dictating whether or not gannets will breed at a particular site. However, Pennycuick *et al.* (1990) noted that colonies of breeding white-tailed tropicbirds *Phaethon leptzirus* are usually downwind of favoured feeding areas.

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