

Is food availability limiting African Penguins *Spheniscus demersus* at Boulders? A comparison of foraging effort at mainland and island colonies

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The African Penguin *Spheniscus demersus* (Vulnerable) formed three new colonies during the 1980s, two on the South African mainland (Stony Point and Boulders) and one on Robben Island. One of the mainland colonies, at Boulders, Simon's Town, is in a suburban area, resulting in conflict with humans. Growth of the Boulders colony was initially rapid, largely through immigration, but has since slowed, possibly as a result of density-dependent effects either on land (where there has been active management to limit the spread of the colony) or at sea. We test the latter hypothesis by comparing the foraging effort of Penguins feeding small chicks at island and mainland sites, and relate this to the foraging area available to birds. Three-dimensional foraging paths of African Penguins were reconstructed using GPS and time–depth loggers. There were no intercolony differences in the rate at which birds dived during the day (33 dives/h), in diving depths (mean 17 m, max. 69 m) or in travelling speeds. The maximum speed recorded was 2.85 m/s, with birds travelling faster when commuting (average 1.18 m/s) than when foraging (0.93 m/s) or resting at sea (0.66 m/s during the day, 0.41 m/s at night). There were strong correlations between foraging trip duration, foraging range and total distance travelled. Foraging effort was correlated with chick age at Robben Island, but not at Boulders. Contrary to Ashmole's hypothesis, birds from Boulders (c. 1000 pairs) travelled further (46–53 km) and foraged for longer (13.2 h) than did birds from Robben Island (c. 7000 pairs) and Dassen Island (c. 21 000 pairs) (33 km, 10.3 h). The mean foraging range also differed significantly between mainland (18–20 km) and island colonies (9 km). The area available to central-place-foraging seabirds breeding on the mainland is typically less than that for seabirds breeding on islands, but the greater foraging range of Boulders birds results in an absolute foraging area roughly twice that of island colonies, and the area per pair is an order of magnitude greater for the relatively small Boulders colony. Ashmole's hypothesis assumes relatively uniform prey availability among colonies, but our results suggest this does not apply in this case. The greater foraging effort of Boulders birds probably reflects reduced prey availability in False Bay, and thus the recent slowing in growth at the colony may be the result of differential immigration rather than management actions to limit the spatial growth of the colony.

The African Penguin *Spheniscus demersus* is listed as Vulnerable, because its current population is c. 10% of that a century ago, and there are ongoing declines in at least parts of its range (Whittington *et al.* 2000,

BirdLife International 2004). During the early 1980s, African Penguins colonized two coastal sites close to Cape Town, the first South African mainland colonies, and re-colonized Robben Island, a former breeding locality abandoned more than two centuries ago due to direct human exploitation (Crawford *et al.* 1995, 1999). The formation of these new colonies coincided

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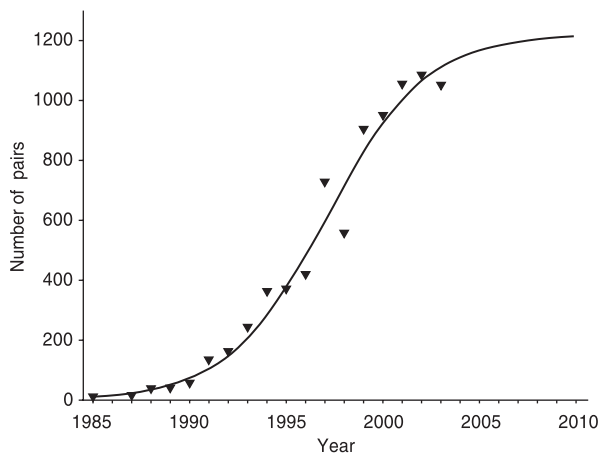


Figure 1. Maximum counts of breeding pairs of African Penguins at Boulders from 1985 to 2003 (Crawford *et al.* 2000, du Toit *et al.* 2004), and projected growth of the colony to 2010 assuming logistic growth: $N_t = K/(1 + \delta e^{-rt})$ where $K = 1215$, $r = 0.387$ and $\delta = 101.7$.

with the collapse of the African Penguin colony on Dyer Island, the largest colony during the late 1970s (Shelton *et al.* 1984), linked to the declining numbers of Cape Anchovy *Engraulis capensis* off the south coast (Crawford 1998). The three new colonies have flourished to varying degrees. Growth of the mainland colony at Stony Point, Betty's Bay, has been interrupted by predation events, with Leopards *Panthera pardus*, Caracals *Felis caracal* and other terrestrial predators killing significant numbers of fully grown birds as well as nestlings (Whittington *et al.* 1996). The other mainland colony at Boulders Beach, Simon's Town, increased from two pairs in 1985 to over 1000 pairs in 2003 (du Toit *et al.* 2004, Fig. 1), largely due to the immigration of first-time breeders from Dyer Island (Crawford *et al.* 2000). The colony at Robben Island has increased most dramatically, reaching a population of more than 7000 pairs in 2002 (Crawford *et al.* 1999, du Toit *et al.* 2004), despite a catastrophic oiling event in 2000 (Nel *et al.* 2003).

The Boulders colony is an important tourist attraction, with some 400 000 visitors to the colony each year (Cape Peninsula National Park unpubl. data), making it both economically and educationally important. This colony occurs within a residential area, which buffers the colony against terrestrial predators, but leads to conflict with some of its human neighbours, who object to the loss of beach access (one of the two main beaches is now closed for recreational use), the increased tourist traffic, and the Penguins' noise and smell. This conflict was exac-

erbated by the fact that many Penguins moved into adjacent gardens to breed. In an attempt to limit the inland spread of the colony, a fence was erected along the inland boundary of the beach reserve in 1996 (Crawford *et al.* 2000). Although the fence is not entirely successful in confining Penguins to the coast, it resulted in an increase in breeding density, and promoted the spread of the colony along the coast (Crawford *et al.* 2000). Erection of the fence coincided with a slowing in the growth of the Boulders colony, a trend that has continued, with little change in the breeding population over the last 3 years (Fig. 1). This has placed the managing agency, South African National Parks, in a difficult position. On the one hand they have to placate neighbours to the reserve, but on the other they are accused of placing limits on population growth of a threatened species.

Another possible reason for the reduced growth of the Boulders colony is that food availability is lower relative to other colonies, resulting in differential immigration. Boulders lies within False Bay, where commercial purse-seine netting, the main fishery competing with penguins, was banned during the early 1980s. However, the pelagic fish that dominate the diet of adult African Penguins (Wilson 1985a, Crawford & Dyer 1995) are highly migratory in the southern Benguela region, moving over much larger scales than the protected area in False Bay (Beckley & van der Lingen 1990, Hutchings *et al.* 1998). Inter-annual variation in numbers of Penguins breeding at Boulders during the 1990s varied in relation to the regional estimate of the spawner biomass of Cape Anchovy, suggesting that food rather than space is limiting the population (Crawford *et al.* 2000). In this paper, we test whether Penguins at Boulders work harder to provision small chicks than do those breeding at Robben and Dassen islands, the two closest island colonies. Foraging effort was measured using novel GPS and time-depth loggers, which allow three-dimensional reconstruction of foraging tracks in unprecedented detail (Ryan *et al.* 2004, Wilson 2004). We also consider the consequences of island vs. mainland breeding on the foraging area available to relatively range-restricted central-place foragers such as penguins.

METHODS

Global Positioning System (GPS) and temperature-depth data loggers (GPS-TDlog), manufactured by Earth & OCEAN Technologies, Kiel, Germany (Gerrit.Peters@t-online.de), were deployed on adult

African Penguins breeding at three colonies near Cape Town, South Africa: Boulders (34°12'S, 18°27'E) from 4 to 17 June 2003, Robben Island (33°47'S, 18°22'E) from 4 to 13 July 2003 and Dassen Island (33°25'S, 18°04'E) from 21 to 24 July 2003. This coincides with the peak breeding season for this region (Cooper 1980). The two island colonies are 50 km apart off the west coast of South Africa, whereas Boulders is on the west coast of False Bay, 90 km 'as the penguin swims' from Robben Island. Loggers were attached to birds being relieved from brooding small- to medium-sized downy chicks (c. 1–6 weeks old) to maximize the probability of retrieval. Chicks were not handled to reduce disturbance to the relieving partner, but chick age was estimated into one of three age classes according to stage of development. Most loggers were deployed in the evening and set to begin recording at 05:00 or 06:00 h the following morning, well before sunrise, when most birds go to sea (Wilson *et al.* 1988). Local sunrise and sunset times (SAST), at the mid-point of each sampling period, were 07:47 and 17:43 h at Boulders, 07:51 and 17:51 h at Robben Island and 07:45 h and 18:04 h at Dassen Island. Birds were recaptured at their nest after they returned from a foraging trip and the logger was removed. Data were downloaded onto a PC, and the logger redeployed on a new bird. No bird was sampled more than once.

The loggers use an active patch antenna to record GPS positions to 0.001 min of latitude and longitude, with an absolute accuracy of c. 5 m in continuous GPS mode and 20 m in intermittent mode (when the device is programmed to switch on at preselected intervals; see Ryan *et al.* 2004 for further details). After deploying devices at various sampling intervals (1 s to 10 min), we selected a 1-min interval as the best compromise between fine-scale accuracy and a high probability of recording a complete foraging trip. All island trips were collected at 1-min intervals, whereas Boulders trips were sampled at 1 s ($n = 4$), 10 s ($n = 4$), 1 min ($n = 7$), 2 min ($n = 4$) and 10 min ($n = 1$). Spatial data collected at different sampling frequencies were corrected using empirical correction factors estimated from comparisons of tracks collected at different sampling rates (Ryan *et al.* 2004). The GPS-TDlog also records water depth to 0.03 bar every 1 s, allowing accurate measurement of dive profiles. Data were stored on 2-Mbyte flash memory.

Each logger was deployed in a hydrodynamic, waterproof housing 96 mm long, 39 × 27 mm in profile, with a total mass of 75 g (c. 2.5% of mean African Penguin mass). The size of the device is

within those previously used on *Spheniscus* penguins (Wilson & Wilson 1995, Luna-Jorquera & Culik 1999), with a cross-sectional area c. 7% that of an African Penguin (Wilson *et al.* 1986). Fitting required two people: one to hold the bird, the other to attach the logger to the bird's lower back, to cause the least impact to the bird's hydrodynamics (Bannasch *et al.* 1994). Five to seven strips of black waterproof Tesa tape were used to hold the logger in place. Attachment took 3–5 min. Trial deployments of logger housings on two captive African Penguins for 4 and 7 days confirmed that the attachment technique had no obvious adverse effects. Both birds continued their normal activities within a few minutes of being released. On recovery, there was no evidence of peck marks on the tape or damage to the birds' plumage. Disturbance and device effects were also controlled for at each locality by estimating trip durations for control birds. These birds were marked without handling using a livestock marker spray applied from c. 0.5 m, and their nests checked 3–4 times daily.

During the study, diet samples were collected from a random sample of ten African Penguins returning to the colonies at Robben Island and Boulders. Samples were collected using the standard flushing procedure used by Marine and Coastal Management (Wilson 1984), and each bird was only flushed once.

Data analysis

We used GPS data to estimate foraging-track length, maximum range (displacement) from the colony and duration of foraging trip. The GPS signal is lost when the logger is submerged, resulting in gaps in foraging tracks during dives, and few fixes were obtained during the high-speed commuting that is typical of departure from the colony (Ryan *et al.* 2004). Minimum foraging trip lengths were estimated by linking all gaps with straight lines. Most trips were complete, but some birds left the colony before their loggers started up, and some logger batteries failed before their birds returned to the colony. Gaps within trips caused by loss of signal typically were fairly short (estimated < 5% of total trip length based on re-sampling GPS data at different frequencies, Ryan *et al.* 2004), but were considerable for incomplete trips (up to at least 55% for birds spending more than 1 day at sea). To avoid biasing against long trips (in terms of both duration and distance), we used minimum estimates of trip length and duration for incomplete tracks, but for most purposes restricted comparisons to 1-day foraging trips, where

most trips were complete or almost complete. We included some tracks where the device started or stopped logging while a bird was apparently commuting from or to the colony. We estimated the missing time assuming a constant commuting speed of 1.7 m/s, close to the maximum speed recorded (see Results) and thus conservative in terms of estimating trip duration.

Dive profiles were analysed using Multitrace (Jensen Software Systems, Laboe, Germany). Dives of ≤ 2 m were considered to be travelling dives (Wilson & Wilson 1990, 1995) and were excluded from analyses of diving effort. With dives defined as > 2 m, dive durations estimated by Multitrace are c. 2–4 s shorter than actual submergence times. A more comprehensive analysis of diving behaviour will be presented elsewhere. Dive data were used to categorize Penguin behaviour at sea into commuting (series of short, shallow dives, typically occurring en route to and from the colony, and often associated with rather linear GPS tracks), foraging (combination of V-, U- and W-shaped dives, see Wilson 1995) or resting (periods between foraging bouts, loosely defined as intervals between dives exceeding 3–5 min). Surface speeds were calculated over at least 1-min intervals, and because this represents a minimum estimate of swimming speed, we compared the fastest 10% of estimates obtained for each activity category.

The position of a dive was taken as the last GPS fix immediately prior to a dive. This was preferred to an interpolated point midway between this point and the first fix following a dive because unacceptably long lags in GPS signal detection sometimes followed dives (see Ryan *et al.* 2004). We plotted the spatial distribution of foraging effort, expressed as total dive time, on a 1×1 -km grid. Where there were long gaps in GPS tracks, dive positions were interpolated along a straight line between successive GPS positions. Only inferred positions within 1 km of a positional fix were retained for analysis. The foraging area potentially available to Penguins at each colony was measured by calculating the total sea area at a range of distances from the colonies (5, 10, 15, 20, 25 and 30 km). This was expressed as area per pair by dividing the area by the maximum colony estimate during the last 5 years (du Toit *et al.* 2004). Foraging volume was estimated by taking an average water depth for each 1×1 -km grid cell from bathymetric databases and charts. Spatial analyses were performed using Arcview GIS 3.2 (Environmental Systems Research Institute, Inc.); other statistical tests were performed in Excel. Mean values below

are given ± 1 sd. Proportional data were arcsine transformed before comparing (Zar 1999). Where a significant difference was detected using ANOVA, differences between means were tested with the Newman–Keuls range test (Zar 1999).

RESULTS

Logger performance and diving behaviour

GPS and time–depth data loggers were deployed on 48 African Penguins. Two loggers were lost due to nest failure at Robben and Dassen islands, where the birds were noticeably more sensitive to disturbance than those at Boulders. It is unclear whether deployment contributed to these nest failures. Nests were deserted after six of 48 deployments where previously an adult had brooded one or more fairly large downy chicks. Initially these nests were assumed to have failed, but visits to the colony late at night found the adults and chicks back at their nests. Disturbance caused by handling adults at these nests apparently caused premature crèching of chicks during the day. The greater susceptibility to disturbance at Robben and Dassen islands resulted in fewer parents of older chicks being sampled at the islands, but there was no significant difference in mean age scores of chicks between island and mainland colonies ($t_{32} = 1.58$, $P = 0.13$). Although only a relatively crude measure of foraging trip length, there were no significant differences in the duration of absences from nests between control and experimental birds at any of the three localities (Table 1). Diet was sampled from one bird equipped with a data logger, which had a full meal of anchovies, indicating that foraging was not significantly impeded by the logger.

Ten loggers were retrieved without recording useful data either due to the bird not leaving the colony or to device failure, and some deployments only recorded dive or GPS data. Spatial data were obtained for 20 birds from Boulders, ten from Robben Island and four from Dassen Island, with dive data from 22, 11 and three birds, respectively. Anchovy was the main prey taken by African Penguins from both Boulders and Robben Island during the study, with more Sardines *Sardinops sagax* at Boulders (Table 2). In total, 10 624 dives > 2 m deep were recorded, with no difference in maximum, mean or median dive depth between Boulders and the two island colonies (Table 3). The deepest dive recorded was 69.4 m by a Penguin from Robben Island ($n = 2853$),

Table 1. Foraging trip duration (h) of African Penguins provisioning small chicks, estimated from nest checks of control and experimental birds three times per day at Boulders, and Robben and Dassen islands.

	Control			Experimental			Significance
	Mean	sd	n	Mean	sd	n	
Boulders	32.8	14.3	117	33.4	12.9	25	$t_{140} = -0.17, P = 0.86$
Robben Island	30.8	12.6	76	27.0	5.8	11	$t_{85} = 0.97, P = 0.33$
Dassen Island	36.3	14.0	57	36.6	26.9	6	$t_{61} = -0.05, P = 0.96$

Table 2. Composition of diet (% by mass) from samples collected at Boulders ($n = 10$) and Robben Island ($n = 10$) during the study.

Species	Boulders	Robben Island
Cape Anchovy <i>Engraulis capensis</i>	72.6	97.8
South African Sardine <i>Sardinops sagax</i>	27.1	1.6
Beaked Sandfish <i>Gonorynchus gonorynchus</i>	0.0	0.6
Onychoteuthid squid	0.3	0.0

Table 3. Foraging parameters for African Penguins making 1-day foraging trips from the mainland colony at Boulders ($n = 14-16$) compared with birds from Robben and Dassen islands combined ($n = 11-14$). Significance was tested with Student's *t*-tests.

Variable	Boulders Mean (range)	Islands Mean (range)	Significance test	<i>P</i>
Departure time	05:10 h (02:18–07:45)	06:44 h (05:05–07:36)	$t_{28} = 3.45$	0.002
Return time	18:10 h (16:48–20:00)	16:56 h (14:54–18:33)	$t_{24} = 2.76$	0.011
Duration (h)	13.18 (10.6–15.8)	10.28 (7.7–13.3)	$t_{23} = 2.77$	0.005
Track length (km)	46.4 (17–62)	33.2 (20–44)	$t_{25} = 3.72$	< 0.001
Foraging range (km)	18.5 (5.8–27.9)	9.4 (5.7–16.8)	$t_{27} = 5.43$	< 0.001
Range/track length (%)	39.5 (31.5–45.6)	28.6 (20.4–38.5)	$t_{25} = 5.53$	< 0.001
Total dive time (min)	269 (95–545)	215 (86–361)	$t_{23} = 1.44$	0.16
Number of dives	353 (210–491)	280 (65–569)	$t_{24} = 1.55$	0.14
Dives per hour*	33.4 (21–44)	32.2 (24–44)	$t_{26} = 0.45$	0.65
% time diving*	47.7 (32–60)	42.9 (30–55)	$t_{26} = 1.98$	0.06
Max. depth (m)	50.6 (29–63)	52.1 (29–69)	$t_{28} = 0.36$	0.72
Mean depth (m)	17.3 (10.9–21.5)	18.0 (12.1–25.0)	$t_{28} = 0.60$	0.55
Median depth (m)	15.1 (9.7–24.7)	15.1 (8.0–23.4)	$t_{28} = 0.04$	0.97
Max. dive duration (s)	106.2 (87–139)	112.1 (89–142)	$t_{28} = 0.78$	0.44
Mean dive duration (s)	52.1 (41–62)	48.0 (38–68)	$t_{28} = 1.51$	0.14

*Confined to daytime, between nautical dawn (c. 07:00 h) and dusk (c. 18:15 h).

with birds from Boulders reaching 62.9 m ($n = 6908$) and those from Dassen Island reaching 49.7 m ($n = 863$). Maximum dive duration was 142 s at Robben Island, 139 s at Boulders and 94 s at Dassen Island. Most dives (98%) occurred during the day (between nautical dawn and dusk), with significantly more night dives by birds from Boulders (3.1%) than those from Robben Island (0.5%; $\chi^2 = 56.8, df = 1, P < 0.001$). All dives at night were shallow (max. 15 m).

Foraging duration and range

Most foraging tracks were complete at Robben Island (7/10) and Dassen Island (3/4), but not at Boulders (only 9/20), where at least four birds remained at sea overnight. One bird from Boulders probably spent two nights away, leaving the colony at 15:45 h and was still 20 km from the colony when its logger stopped recording at 16:30 h the following afternoon. By comparison, at most one bird from

Robben and Dassen islands remained at sea overnight: this bird was 2 km off Robben Island when its logger started at 05:00 h (and so could have left the colony early that morning), but it returned to the island at 11:55 h, which is surprisingly early for a bird making a 1-day trip. Apart from these two birds, all others left the colonies in the early morning (02:30–07:40 h) and returned in the afternoon or evening (14:55–20:00 h). The average departure time for Penguins from Boulders (05:10 h \pm 92 min) was more than 2.5 h before sunrise, earlier than birds from Robben and Dassen islands (06:44 h \pm 46 min, Table 3). Boulders birds also returned later (18:10 h \pm 62 min) than birds from Robben and Dassen islands (16:56 h \pm 73 min, Table 3). These differences in departure and arrival times resulted in significantly shorter foraging trip durations for island-breeding Penguins than for Penguins from Boulders, even when only considering 1-day foraging trips (Table 3). However, there was no difference between colonies in trip duration as measured by nest checks of control birds (ANOVA, $F_{2,290} = 2.6$, $P = 0.074$).

There were no significant differences in foraging effort between Penguins from Robben and Dassen islands (e.g. trip duration $t_{12} = 1.42$, $P = 0.19$; track length $t_{12} = 0.18$, $P = 0.86$; foraging range $t_{12} = 0.33$, $P = 0.75$; number of dives $t_{12} = 0.32$, $P = 0.76$; total dive time $t_{12} = 0.35$, $P = 0.73$), so data for birds from the two islands were pooled. Comparing Boulders with the island colonies, the longer trip durations at Boulders were associated with greater maximum foraging ranges (18.5 \pm 5.3 km, $n = 16$ vs. 9.5 \pm 3.2 km, $n = 11$) and total trip distances (46 \pm 11 km vs. 33 \pm 8 km, Table 3). These differences were even more marked if multiday trips were included, increasing the maximum foraging range for birds from Boulders to 20.3 \pm 6.3 km (max. 34 km, $n = 20$, $t_{31} = 5.76$, $P < 0.001$), with total trip distances increasing to 53 \pm 18 km ($t_{31} = 3.76$, $P = 0.0001$). Significant results were obtained for these parameters if Boulders birds were compared with those from Robben Island alone. There was a highly significant relationship between trip duration and distance travelled (Fig. 2), and between distance travelled and maximum range from the colony (Fig. 3). Maximum foraging range was also correlated with trip duration:

$$\text{maximum range (km)} = 1.98 * \text{duration (h)} - 8.72$$

$$(r_{23} = 0.72, P < 0.001),$$

but less strongly than total distance travelled (Fig. 2). Trip distance and range were significantly correlated

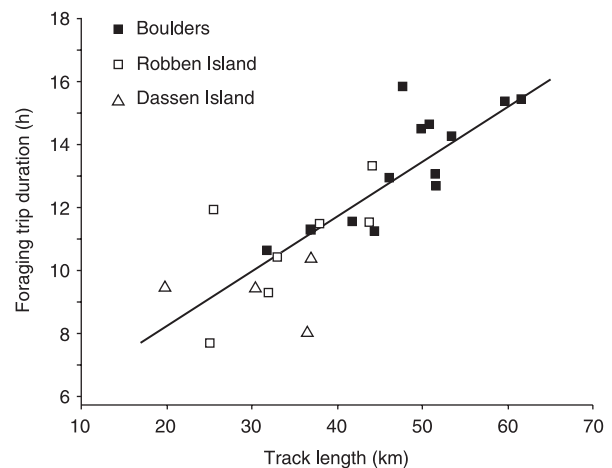


Figure 2. The relationship between foraging trip duration and distance travelled by African Penguins on 1-day foraging trips to provision young chicks at three colonies off the Western Cape, South Africa. The line shows the best fit regression for all colonies combined: distance (km) = 3.98 * duration (h) - 6.01 ($r_{23} = 0.83$, $P < 0.001$). Gaps in GPS tracks were linked by straight lines, and missing time for almost complete tracks extrapolated assuming commuting at 1.7 m/s (see Methods for details).

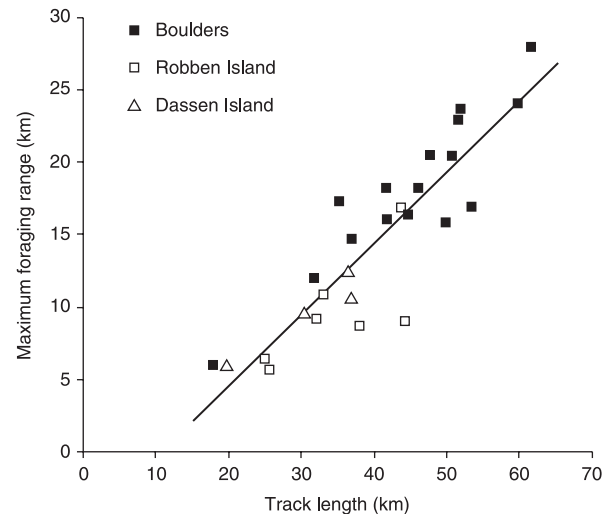


Figure 3. The relationship between distance travelled by African Penguins on 1-day foraging trips and the maximum distance from the colony. Conventions as in Fig. 2: distance (km) = 0.492 * track length (km) - 5.34 ($r_{24} = 0.91$, $P < 0.001$).

with chick age at Robben Island ($r_8 = 0.77$, $P = 0.01$; $r_8 = 0.66$, $P = 0.03$, respectively), with duration almost significant ($r_8 = 0.58$, $P = 0.08$), but there were no significant effects of chick age at Boulders ($r_{18} = 0.15$, $P = 0.54$; $r_{18} = 0.21$, $P = 0.20$; $r_{18} = 0.17$, $P = 0.48$, respectively).

Most other foraging parameters did not differ significantly between colonies (Table 3), irrespective of whether all trips or just 1-day trips were compared. Birds from Boulders on 1-day trips dived for 25% longer and made 20% more dives on average (Table 3), but these differences were not significant unless multiday trips were included, when Boulders birds dived for significantly longer per trip (315 ± 91 min, $n = 18$) than island birds (233 ± 92 min, $n = 12$, $t_{28} = 2.39$, $P = 0.02$). There was also a greater tendency for Boulders birds to make more dives per trip (374 ± 124 , $n = 18$) than island birds (294 ± 120 , $n = 12$, $t_{28} = 1.75$, $P = 0.09$) when multiday trips were included. The difference would probably be significant if a greater proportion of Boulders trips were complete.

African Penguins from Boulders remained within False Bay, within 35 km of the colony, despite staying away from their nests for up to 2 days. Birds from Robben and Dassen islands foraged even closer to their colonies: within 17 km (Fig. 4, Table 3). Foraging activity by Penguins from Boulders was concentrated in the centre of False Bay, towards the entrance of the Bay (Fig. 4). These birds initially followed rather

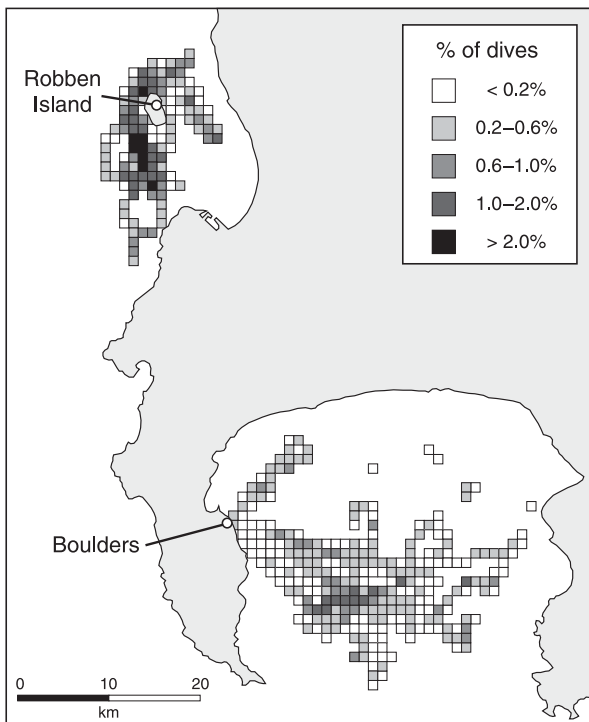


Figure 4. Distribution of foraging effort (proportion of total dive time > 2 m deep) by African Penguins breeding at Boulders ($n = 20$ trips) and Robben Island ($n = 11$) plotted on a 1×1 -km grid.

linear paths for 1–2 h, with 18 of 20 birds heading southeast or east-southeast. The two exceptions headed northeast or east-northeast. Once foraging began, the path became more sinuous before commuting, again in a fairly linear manner, back to the colony (see Ryan *et al.* 2004 for an example of a single track). By comparison, Penguins from Robben Island followed more sinuous routes throughout their trips, with nine out of ten circumnavigating the island anticlockwise. Robben Island birds started diving sooner after leaving the colony (20 ± 21 min, range 1–69, $n = 10$) than did birds from Boulders (41 ± 25 min, range 12–75, $n = 12$, $t_{20} = 2.10$, $P = 0.05$). The main feeding areas for Robben Island birds were 3–10 km from the colony, predominantly south and west of the island, whereas Boulders birds mainly foraged 14–27 km from their colony (Fig. 4). The few tracks of Penguins breeding on Dassen Island were generally similar to those from Robben Island (Figs 2 and 3), but none circumnavigated the island, even though Dassen Island is smaller than Robben Island. The more sinuous tracks of island birds, lacking a clear linear commuting component, is reflected in the smaller proportion of total trip distance accounted for by the maximum displacement from the colony (only 72% that of Boulders birds, Table 3).

Surface speed

Surface speed estimates varied greatly, but were higher during the day (Fig. 5, Table 4; $t_{6485} = 34.41$, $P < 0.001$ for all data and $t_{647} < 32.7$, $P = 0.001$ for fastest 10%). There was no significant difference in maximum speeds during the day estimated for birds from Boulders (top 10% average 1.50 ± 0.23 m/s, $n = 492$) and those from the islands (1.52 ± 0.14 m/s, $n = 185$, $t_{674} = 1.01$, $P = 0.31$). There was a tendency for higher maximum speeds around dawn and, to a lesser extent, dusk, corresponding with commuting (Fig. 5). Restricting the analysis to birds from Boulders, where commuting phases were clearly evident, average speed estimates were greater during commuting and foraging than during rest periods between diving bouts ($F_{2,4913} = 477.6$, $P < 0.001$ for all data combined). Comparing the fastest 10% estimates, commuting birds travelled faster than foraging birds, and both were faster than resting birds ($F_{2,488} = 178.6$, $P < 0.001$, Table 4). Treating all estimates equally ignores differences in sample intervals, and typically biases against higher speeds (when birds spend more time underwater, and thus obtain fewer

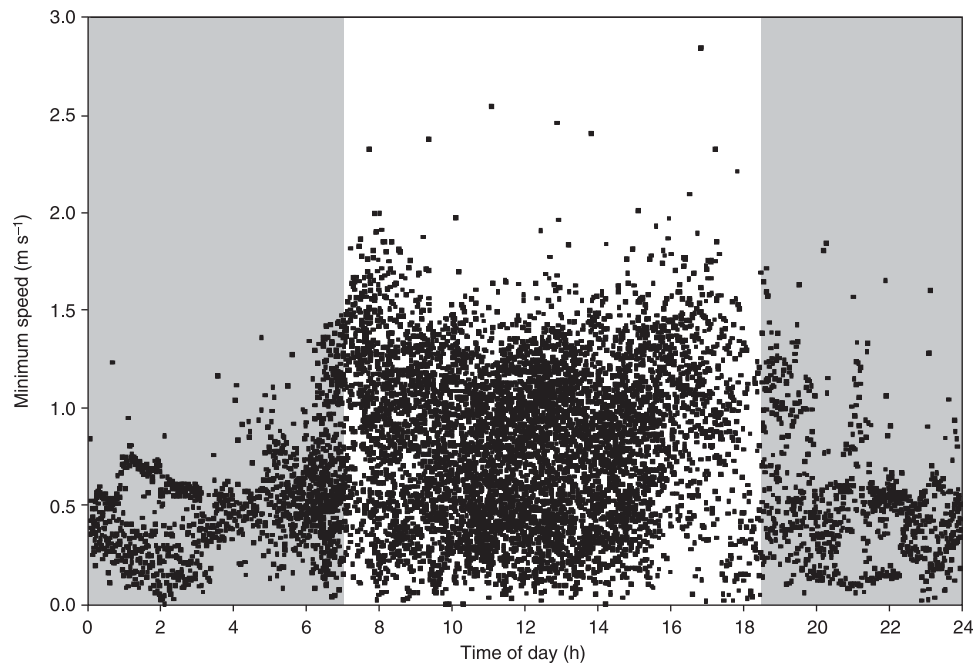


Figure 5. Surface speed estimates based on successive GPS positions from 34 African Penguins provisioning for small chicks in relation to the time of day ($n = 8335$). Shaded area = night (between nautical dusk and dawn).

Table 4. Surface speed (m/s) estimates for African Penguins from Boulders provisioning small chicks. Pooled estimates sum all displacements and all time intervals to obtain an average speed estimate. The fastest 10% estimates recorded are averaged to characterize the upper limits associated with each activity.

Activity	n	All data mean \pm sd (range)	Pooled estimate	Fastest 10% mean \pm sd
Day (overall)	4916	0.82 ± 0.39 (0.00–2.85)	0.91	1.50 ± 0.23
Commuting	393	0.93 ± 0.42 (0.13–2.85)	1.18	1.65 ± 0.23
Foraging	3405	0.90 ± 0.37 (0.00–2.55)	0.93	1.50 ± 0.18
Resting	1118	0.52 ± 0.31 (0.00–1.82)	0.66	1.18 ± 0.15
Night (overall)	1571	0.46 ± 0.23 (0.00–1.85)	0.48	0.90 ± 0.22
Resting	1485	0.44 ± 0.20 (0.00–1.65)	0.41	0.80 ± 0.20

GPS fixes). This bias can be reduced by estimating the speed associated with each activity as the sum of all displacements over the total time, resulting in higher average speed estimates for all activities except resting at night (Table 4). The maximum speed estimate (2.85 m/s, attained by a bird covering 210 m in 74 s) occurred shortly before coming ashore, and was associated with a series of shallow travelling dives. Three birds tracked at sea throughout the night exhibited almost linear GPS tracks at a sedate 0.1–0.7 m/s, apparently drifting (Fig. 5). Periods of irregular movement (3–6% of night) coincided with diving activity and higher surface speeds (0.9–1.8 m/s). Birds resting at night moved more slowly than birds

resting during the day (Table 4, $t_{2600} = 8.27$, $P < 0.001$), and this difference was even more marked if only the fastest 10% of estimates were compared (Table 4, $t_{259} = 16.69$, $P < 0.001$).

The potential foraging area available to African Penguins differed among the three study colonies as a result of differences in coastal topography. Foraging area is greater close to colonies at both islands than at Boulders, where birds are constrained to travel east by the mainland (Fig. 4), and this difference increases with increasing foraging range (Fig. 6). By travelling 10 km, the mean foraging range recorded for Penguins from island colonies, island birds can access $c. 250 \text{ km}^2$ of coastal waters, compared with

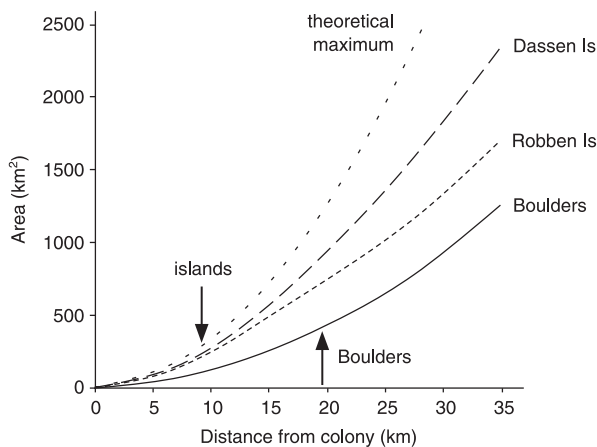


Figure 6. Potential foraging area available to African Penguins from Boulders compared with nearby island colonies. Arrows depict the average foraging ranges of birds from Boulders and the two island colonies.

only 115 km² from Boulders (Fig. 6). The actual foraging range of Boulders birds (18–20 km) makes available c. 400 km², almost twice that of island birds (Fig. 6). This difference is an order of magnitude greater when expressed as area per pair: c. 40 ha/pair at Boulders (1000 pairs), compared with 3.6 ha/pair for Robben Island birds (7000 pairs) and 1.2 ha/pair for Dassen Island birds (21 000 pairs). Even if Boulders birds only ranged as far as island birds, they would have 3–10 times as much foraging area per pair (11.5 ha) as birds from Robben and Dassen islands. In our samples, birds from Robben dived in a total area of 120 km² whereas Boulders birds utilized 276 km² (Fig. 4). This was not simply a result of deeper water around the islands. Average water depth in which Boulders Penguins dived was 45.3 m, compared with 41.5 m for Robben Island, and the total volume of water explored by Boulders birds (13.1 km³) was almost three times that by Robben Island birds (4.6 km³).

DISCUSSION

Device effects

This study reports the first use of GPS data loggers to compare foraging effort between Penguins from different colonies. There was no evidence that the devices significantly affected the foraging performance of African Penguins, although the power to detect any impacts was low. Checking nests 3–4 times per day gives only a crude index of foraging trip dura-

tion, especially if Penguins spend varying lengths of time on the beach before returning to their nest. A study of the diving ecology of Humboldt Penguins *Spheniscus humboldti* found foraging trips 11–30% longer in birds equipped with time–depth recorders compared with trips of control birds measured by continuous watches at landing beaches (Taylor *et al.* 2001). Our checks at nests were too infrequent to detect impacts of this magnitude, as indicated by the much longer trip estimates made using nest checks (Table 1) and the failure to detect intercolony differences in foraging trip duration among control birds.

The GPS-TD loggers used in our study probably affected foraging performance to some extent (cf. Wilson *et al.* 1986, Culik *et al.* 1994), but they were smaller than devices previously used on African Penguins (Wilson & Wilson 1995), and did not prevent birds foraging successfully. We did not weigh birds before and after deployment to reduce disturbance, but similar trials with Humboldt Penguins found no significant effect of a larger logger (Luna-Jorquera & Culik 1999). The foraging behaviour we measured accords with what is known about the foraging ecology of African Penguins (see below), including information obtained without the use of loggers, such as trip duration based on colony observations (Wilson & Wilson 1990) and foraging range inferred from observations at sea (Wilson *et al.* 1988). Fortunately, any device effect should be constant, and thus not compromise the intercolony comparison of foraging effort. If anything, Boulders birds should have performed better, because they appeared to be more tolerant of disturbance caused by device deployment.

Comparison with previous studies of foraging ecology

Our results show a close correlation between foraging trip duration, distance travelled and maximum foraging range. Although the sample size was smaller and included a much larger range of temporal and spatial scales, African Penguins radiotracked from St Croix Island, Algoa Bay (Heath & Randall 1989), provided an almost identical relationship to ours between total distance travelled and foraging duration (cf. Fig. 2):

$$\text{distance travelled (km)} = 4.44 * \text{duration (h)} - 6.20$$

$$(r_0 = 0.79, P = 0.004).$$

The similarity of these regressions is all the more remarkable given that they were estimated using

different techniques, and probably with quite severe device effects associated with the radio antennae used by Heath and Randall (Wilson *et al.* 2004). By comparison, Humboldt Penguins apparently travel less far for the same amount of time at sea (distance (km) = $2.24 * \text{duration (h)} + 0.69$; Luna-Jorquera & Culik 1999). This estimate was made using a speed turbine attached to the birds' backs, however, and thus is not directly comparable, as it includes vertical movement during diving, but excludes surface movement.

The St Croix tracks also gave a significant regression between total distance travelled and maximum distance from the colony:

$$\text{maximum range (km)} = 0.217 * \text{track length (km)} + 12.97 \quad (r_8 = 0.74, P = 0.014)$$

but the coefficient was less than half that in our study (0.492), with a greater intercept (Fig. 3). This difference presumably results from the longer trips by St Croix birds, which included several multiday trips. Incorporating multiday trips into our data set also resulted in a reduced coefficient (range = $0.350 * \text{track length} + 0.39$; $r_{29} = 0.846, P < 0.001$), although this was also affected by the multiday trips being incomplete. Similar relationships between trip duration and distance have been demonstrated for Adélie Penguins *Pygoscelis adeliae* (Wilson 1995) and other seabirds (e.g. Northern Gannets *Morus bassanus*, Hamer *et al.* 2000), and suggest that trip duration can be a reasonable proxy for foraging effort and range in African Penguins. Trip duration needs to be measured accurately, however, posing problems for direct observation of trip duration in African Penguins, which often depart and return during darkness, and breed in relatively large colonies, making individual recognition difficult (cf. Taylor *et al.* 2001). They also spend varying amounts of time idling on the beach and commuting to and from the shore and their nest-site. Nest checks are too coarse a measure for birds feeding small chicks, but they may be useful for longer trips at other stages of the breeding cycle. A salt-water switch attached to a small logger may be a useful technique to compare foraging effort between colonies.

Swimming speeds of African Penguins have been measured using a variety of techniques (Wilson 1985a, Heath & Randall 1989), and although they can attain speeds of up to 5 m/s during short bursts (Wilson 1985a), they typically swim underwater at around 2 m/s (Wilson *et al.* 1989), and travel more slowly on the surface. Wilson (1985a) estimated that commuting African Penguins travel at 1.2 m/s, based

on a dive-to-surface ratio of 1 : 0.8 and surface swimming speed of 0.4 m/s. This accords closely with our average commuting speed estimates (Table 4), although it is apparent that Penguins occasionally move more rapidly (> 1 m/s) while on the surface (*contra* Wilson & Wilson 1995). Heath and Randall (1989) estimated slightly higher commuting speeds (averaging 1.5 m/s on leaving the colony and 1.7 m/s when returning), and also had higher average foraging (1.2 m/s) and night drifting speeds (0.8 m/s) than our birds (Table 4). It is unclear whether these are real differences, linked to their longer foraging trips (cf. Pütz *et al.* 2002), or an artefact of the crude positional accuracy of radiotracking at sea.

The diving behaviour exhibited by birds in this study agrees well with previous estimates for African Penguins (Wilson 1985a, Wilson & Wilson 1990). African Penguins rely on daylight to see and catch their prey (Wilson 1985a, 1985b), hence the virtual absence of nocturnal feeding activity (Wilson & Wilson 1995). Birds from St Croix Island radiotracked at night spent less than 6% of their time diving (Heath 1985). The proportion of time that tracked birds spent diving during the day (average 45%, range 30–60%) is intermediate between that estimated for birds from Marcus Island ($37 \pm 18\%$, Wilson *et al.* 1989) and St Croix Island (54%, Heath 1985). The maximum dive depths we recorded (60–70 m) are less than the absolute maximum recorded for African Penguins using capillary depth gauges (130 m; Wilson 1985a), but are consistent with the modal maximum depth of 50–60 m (Wilson & Wilson 1990), with most dives shallower than 30 m (Wilson 1985a).

Intercolony differences

The main difference between colonies in our study was that birds from Boulders made foraging trips of longer duration and covering a larger area than did birds from Robben and Dassen Islands. There appears to be a significant difference in trip duration between Penguins provisioning small chicks on the west coast, where most undertake 1-day trips lasting less than 12 h (Wilson & Wilson 1990) and at St Croix Island, Algoa Bay, on the south coast of South Africa, where most trips are more than 24 h (Heath 1985). Tracked birds from Robben and Dassen islands behaved like African Penguins with small chicks at Marcus Island on the west coast of South Africa, where most depart at 08:00 h and arrive at 17:30 h (Wilson *et al.* 1988), ranging on average

11 km (trip length *c.* 30 km; Wilson & Wilson 1990). By comparison, Penguins from Boulders behaved in a manner intermediate between west coast and south coast birds (Heath & Randall 1989). Foraging trips increase in duration and length as chicks get larger on the west coast, with Penguins provisioning small chicks on Marcus Island ranging 15 km (trip length *c.* 39 km) for medium-sized chicks (Wilson & Wilson 1990). This may have influenced the longer trips from Boulders to some extent, because more birds with older chicks were sampled, but there was little relationship between chick age and trip duration or length. Boulders birds did not travel as far as Penguins breeding at St Croix Island, on the south coast, which ranged *c.* 40 km from the colony, travelling an average of *c.* 100 km (Heath & Randall 1989). These studies used different techniques, and there is some concern that device effects might have contributed to the long trips in some birds from St Croix (cf. Wilson *et al.* 2004), but differences in prey distribution and availability together probably result in longer trips for south-coast Penguins (Heath 1985, Heath & Randall 1989).

The linear tracks of African Penguins commuting to and from Boulders are similar to the tracks of birds from Marcus Island, Saldanha Bay, where most Penguins commute to shelf waters outside the bay (Wilson & Wilson 1988, 1990, Wilson *et al.* 1991) and from St Croix Island, Algoa Bay, where they commute to productive waters south of Cape Recife (Heath & Randall 1989). By comparison, birds from Robben and Dassen islands had less well-defined commuting phases, having sinuous tracks and starting to forage closer to the colony. This difference was not a consequence of shallower waters close to Boulders; birds from all three colonies encounter 30-m-deep water approximately 1 km from shore. A more plausible explanation is that prey are typically encountered closer to the offshore islands than they are to either mainland colonies, or colonies at islands inside bays.

Ashmole's (1963) hypothesis predicts that colony size should affect the foraging effort of central-place foragers such as seabirds. In general, birds from larger colonies are predicted to have to work harder to obtain the same amount of food, due to density-dependent competition caused either by localized prey depletion or reduced prey availability due to interference (Lewis *et al.* 2001). Empirical support for Ashmole's hypothesis comes from the relationships between colony size and spacing (Furness & Birkhead 1984), reproductive success and chick growth (Hunt *et al.*

1986), as well as direct measures of foraging effort (Lewis *et al.* 2001) and reduced prey density close to colonies (Birt *et al.* 1987). Consequently, one would expect birds from the relatively small Boulders colony to obtain their foraging requirements in shorter foraging trips, closer to the colony than birds breeding in the larger colonies on Robben and Dassen islands. Island birds benefit from having a greater foraging area within the same foraging radius than do mainland birds, but this effect cannot explain the greater foraging effort exerted by Boulders Penguins, because the disparity in colony sizes more than offsets the reduced foraging area.

Ashmole's hypothesis assumes that prey availability differs little between colonies. The colonies studied here are relatively close together (50 km between Dassen and Robben islands, and 90 km between Robben Island and Boulders as the penguin swims). Penguins breeding at Robben Island have been tracked to both Dassen Island and Boulders (R.J.M. Crawford unpubl. data), and incubating birds from Dassen Island forage outside the mouth of False Bay (C. le Bohec unpubl. data). Birds from the three colonies thus probably experience similar foraging conditions during at least part of the breeding season. However, pelagic fish are highly migratory and are patchily distributed within the Benguela upwelling system (Hutchings *et al.* 1998). Anchovies and sardines move south from the west coast onto the Agulhas Bank to spawn during spring and summer. The eggs and larvae are then transported by north-flowing jet currents into productive nursery areas associated with upwelling cells along the west coast (Beckley & van der Lingen 1990, Hutchings & Field 1997, Hutchings *et al.* 1998). Robben and Dassen islands are both situated on the migration routes of sardine and anchovy as they move to and from their spawning grounds, whereas Boulders lies in False Bay, off the main migration route. The fact that almost all Boulders Penguins headed southeast towards the mouth of False Bay suggests that pelagic fish are encountered more predictably in this area, closer to the main fish migration route. It thus seems likely that the longer foraging trips, in terms of both time and distance, exhibited by Penguins from Boulders indicate reduced prey availability in False Bay compared with the west coast around Robben and Dassen islands, at least during our study period.

Most of the growth in population size at the newly founded colonies at Robben Island and Boulders has been the result of immigration, with observed annual growth rates of up to 60%, greatly exceeding

the fastest rate of growth possible due to reproduction (Crawford *et al.* 2000). Compared with Boulders, where the maximum colony count is 89% of the predicted carrying capacity (Fig. 1), the colony at Robben Island has only reached 63% of the carrying capacity (assuming logistic growth; $K = 11\,425$, $r = 0.212$ and $\delta = 50.9$). This suggests that Robben Island attracts a higher proportion of immigrants than Boulders, and that Boulders has become less attractive to young Penguins selecting a breeding site for the first time. Our data are limited to short periods in a single season, and thus one has to be cautious when drawing general conclusions about differences in foraging effort between colonies. However, it is tempting to speculate that the relatively poor foraging conditions we inferred in False Bay may account for the observed slowing in the growth of the Boulders colony. Food availability determines the proportion of adult African Penguins breeding each year (Crawford & Dyer 1995, Crawford *et al.* 1999) and their breeding success (Adams *et al.* 1992, Crawford & Dyer 1995). It may also influence colony growth; during the late 1990s there was a correlation between the growth of the Boulders colony and anchovy biomass estimates for the southern Benguela region (Crawford *et al.* 2000). More data are needed on Penguin foraging effort, especially in relation to fine-scale prey distribution and relative abundance. The GPS-TD loggers used in this study offer a practical way to measure Penguin foraging effort. If our results are typical of foraging conditions at the three sites studied, it is plausible that the slowing in population growth rate at Boulders has resulted from the differences in food availability rather than any management actions on land.

We thank Gerrit Peters for providing data loggers and technical advice, and Nick Lindenberg and Laurent Drapeau for assistance with data analysis. Monique Ruthenberg, Crecilda van den Berg, Chris Clift, Lennox Zosela and Marta de Ponte provided assistance in the field, and Bruce Dyer helped with diet collection and analysis. Permission to work on African Penguins was obtained from Marine and Coastal Management, Department of Environmental Affairs and Tourism, Robben Island Museum, Cape Nature Conservation and Cape Peninsula National Park, with ethical approval of the University of Cape Town's and South African National Park's animal ethics committees. Accommodation was kindly provided by the Everingham family at Boulders. Financial support was obtained from the Centre National de la Recherche Scientifique, the South African National Research Foundation, the University of Cape Town, Bob Blundell, Earthwatch and an Ocean Basket Scholarship to S.L.P.

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Received 24 August 2004;
revision accepted 10 June 2005.