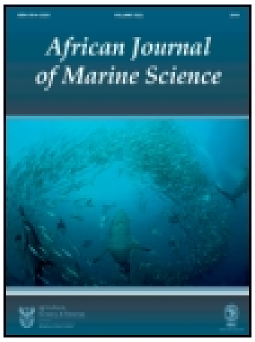

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Diving behaviour of African penguins: do they differ from other *Spheniscus* penguins?

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African penguins *Spheniscus demersus* closely resemble Magellanic *S. magellanicus* and Humboldt *S. humboldti* penguins and have similar breeding and feeding ecologies. Adults feed on pelagic schooling fish in continental shelf waters, but African penguins have been reported to have shallower dive angles and remain submerged longer for dives to a given depth than their congeners. The few data for African penguins were gathered using relatively large time-depth recorders. We measured diving behaviour of 36 African penguins provisioning small chicks at three colonies near Cape Town, South Africa. Maximum and mean dive depths were 69m and 14m respectively. Diving took place mainly during the day. Although dive depths differed between colonies, there were no significant differences in dive duration or maximum, median or mean depth. Total dive duration, descent time, bottom time, ascent time and dive angle all were strongly correlated with the maximum depth attained. The diving behaviour of African penguins is similar to that of its congeners. Diving performance probably was compromised by the data-logger used in the previous study. Comparative data from Humboldt penguins also indicate potential biases in an earlier study of this species. Care is needed when comparing the diving performance of penguins measured using different loggers.

Keywords: African penguin, dive angle, dive depth, dive duration, logger impacts, *Spheniscus*

Introduction

The use of data-loggers that can be mounted on foraging animals has revolutionised the study of feeding ecology, especially for marine animals (Boyd 1997, Krauss 1998, Wilson *et al.* 2002a, Ropert-Coudert and Wilson 2005). Much of the pioneering development of these devices was conducted on African penguins *Spheniscus demersus* (e.g. Wilson and Bain 1984a, 1984b), but in recent years attention has been focused on other species. The first generation of devices stored depth data cumulatively using photometric techniques (Wilson and Bain 1984a, Wilson *et al.* 1989), which albeit ingenious lacked the fine-scale resolution of modern digital devices. Much of what is known about the diving ecology of African penguins is derived from these early devices (e.g. Wilson 1985, Wilson and Wilson 1990), and has been broadly supported by more recent studies of congeners, notably Magellanic (*S. magellanicus*) (Peters *et al.* 1998, Walker and Boersma 2003) and Humboldt (*S. humboldti*) penguins (Luna-Jorquera and Culik 1999, Taylor *et al.* 2002). However, only one study of African penguins has used digital time-depth recorders (TDRs) to store detailed data on dive structure (Wilson and Wilson 1995). The relatively small sample of dives obtained differed from the data recorded for Magellanic and Humboldt penguins in two significant respects: (1) African penguins appear to dive much longer in relation to water depth than their close relatives, and (2) dive angles of African penguins are considerably shallower than those of their congeners (Peters *et al.* 1998, Luna-Jorquera and Culik 1999). Peters *et al.* (1998) considered these differences to be intriguing, but could not rule out the possibility that they were simply extreme site-specific effects, citing within-species variability in dive behaviour recorded for Magellanic penguins. They called for the deployment of TDRs at multiple sites to assess the extent of within-species variability, and thus place into context the apparent inter-species variability.

In this paper, we report the diving behaviour of African penguins at three sites around Cape Town, South Africa, and test for inter-colony differences. We then test whether the structure of African penguin dives differs consistently from that of their congeners. We include some comparative data for Humboldt penguins collected by AS, because previously published information for this species (Luna-Jorquera

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and Culik 1999) were not analysed appropriately, and also may have been influenced by large-device size.

Material and Methods

Combined temperature, depth and GPS loggers (GPS-TDlog) manufactured by Earth&Ocean Technologies, Kiel, Germany, were deployed on adult African penguins breeding at three colonies around Cape Town, South Africa, during June–July 2003. Most data were obtained from the mainland colony at Boulders (34°12'S, 18°27'E) and Robben Island (33°47'S, 18°22'E), with only three birds providing data from Dassen Island (33°25'S, 18°04'E). The two island colonies are 50km apart on the west coast of South Africa, whereas Boulders is on the west coast of False Bay, 90km as the penguin swims from Robben Island. Loggers were attached to birds being relieved from brooding small- to medium-sized downy chicks to maximise the probability of retrieval. Most loggers were deployed in the evening and set to begin recording at 05:00 or 06:00 the following morning (sunrise c. 07:50). Birds were recaptured at their nest after they returned from a foraging trip and the logger removed. Data were downloaded onto a PC, and the logger redeployed on a new bird. No bird was sampled more than once.

The loggers recorded water depth using a pressure transducer accurate to 0.03 bar (c. 0.3m) every 1s, allowing accurate measurement of dive profiles. They also use an active patch antenna to record GPS positions to 0.001 minutes of latitude and longitude, with an absolute accuracy of c. 5m in continuous GPS mode and 20m in intermittent mode (see Ryan *et al.* 2004 for further details). Data were stored on 2-Mbyte flash memory. Loggers were housed in a hydrodynamic, waterproof shell 96mm long, 39mm x 27mm in profile (sectional area 1 053mm^2, c. 7% of African penguin sectional area; Wilson *et al.* 1986) with a total mass of 75g (c. 2% of mean African penguin mass). Loggers were mounted on the penguin's lower back, where they cause the least impact to the bird's hydrodynamics (Bannasch *et al.* 1994), using 5–7 strips of black waterproof Tesa tape (Wilson *et al.* 1997). Attachment took 3–5min. Trial deployments of logger housings on two captive African penguins for 4 days and 7 days confirmed that the attachment technique had no obvious adverse affects. The housings were largely ignored after an initial bout of preening, and there was no damage to the plumage on removal of the housings. Based on regular nest checks, trip durations of experimental birds were not significantly longer than those of control birds, and experimental birds fed successfully, suggesting that device impacts were limited (Ryan *et al.* 2004).

Statistical analyses

Dive profiles were analysed using MultiTrace (Jensen Software Systems, Laboe, Germany). Dives ≤2m were considered to be travelling dives (Wilson 1995) and excluded from analyses of diving effort. Because the 2m 'threshold' is rather arbitrary, we explored the consequences of increasing the threshold to 3m, 4m and 5m. With dives defined as >2m, dive durations estimated by MultiTrace are c. 2–4s shorter than actual submergence times, and in some cases considerably shorter, because penguins frequently remained 0–1m below the surface for 10–15s immediately after ascending (although they may sometimes have surfaced very briefly to breathe). Dives were categorised as either V- or U-shaped, corresponding with search and feeding dives respectively (Wilson 1995, Wilson and Wilson 1995). U-shaped dives (including W-shaped dives) consist of a descent phase, a bottom phase, where the bird presumably pursues prey, and an ascent phase (Wilson 1995). MultiTrace objectively defines these phases, and reports their durations as well as calculating the average rate of vertical ascent and descent. Dive angles were estimated assuming a constant underwater swimming speed of 2.1m s^{-1} (Wilson and Wilson 1995, Peters *et al.* 1998, Wilson *et al.* 2002b).

We compared differences in dive parameters between colonies at the level of the individual by calculating mean dive parameters for each bird, and testing for significant differences between birds from Boulders and island colonies. Only birds that made at least 100 dives were included in these comparisons, to ensure an adequate sample of dives (mean 336 ± 128 dives per bird). However, dive data obtained from all birds were included in analyses relating dive parameters to maximum dive depth, with data pooled among colonies. Various authors have preferred different models relating dive parameters to maximum dive depth (e.g. Wilson and Wilson 1995, Peters *et al.* 1998, Luna-Jorquera and Culik 1999). We used the models that consistently gave the best coefficient of determination (r^2). Regression lines were estimated in Excel, using the Solver tool to estimate non-linear best fits.

The only published information regressing dive characteristics with maximum dive depth for Humboldt penguins (Luna-Jorquera and Culik 1999) contains some anomalous results (e.g. using a log-log regression to relate vertical dive rate to maximum dive depth, but a linear regression between dive angle and dive depth). Consequently, we compared the African penguin data with diving behaviour of Humboldt penguins collected at Pájaros Island (29°35'S, 71°33'W), 40km north-west of Coquimbo, North-Central Chile, during November–December 2001 (AS, unpublished data). Five adults provisioning small chicks were equipped with LTD 100 data-loggers (Lotek Marine Technologies Inc., Canada), which recorded water depth every 2s. These loggers weigh only 22g and are cylindrical, 57mm long and 18mm in diameter (sectional area 255mm^2). Dive data from these birds (n = 6 409 dives >2m) also were analysed using MultiTrace and summarised in the same way as the African penguin data.

Results

Fine-scale dive data were obtained for 10 624 dives >2m deep by 35 African penguins: 21 from Boulders (n = 6 908 dives), 11 from Robben Island (n = 2 853) and three from Dassen Island (n = 863). Increasing the dive 'threshold' to 3m decreased the number of dives by 5%, to 4m by 10% and to 5m by 15%. Most penguins studied had foraging trips lasting <1d, departing in the early morning and returning

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in the evening, but at least four birds from Boulders remained at sea overnight. Few dives were obtained from two birds from Boulders that were tracked mainly at night, and one each from Robben and Dassen islands had short data series; these individuals were excluded from comparisons between individuals from different colonies.

Almost all dives (98%) took place during the day, with the few dives during the night confined to shallow depths, mainly <10m (Figure 1). Maximum dive depths increased rapidly at dawn, and decreased equally rapidly at dusk, with some evidence of bimodality in timing of the deepest dives at both Boulders and Robben Island (Figure 1). Overall, there was little difference in diving behaviour between birds from Boulders and Robben Island, with birds from Dassen Island similar to those from the other two colonies (Table 1). Only descent rate differed significantly between Boulders and Robben Island (Table 1), with the difference between mean colony values 12%. There was no difference in dive depths between colonies (either maximum, mean or median; Table 1), but the frequency distribution of dive depths differed, with fewer dives <10m and more to 20–30m at Boulders (Figure 2). The deepest dive recorded was 69.4m by a penguin from Robben Island, with Boulders birds reaching 62.9m and the small sample of Dassen Island birds reaching 49.7m.

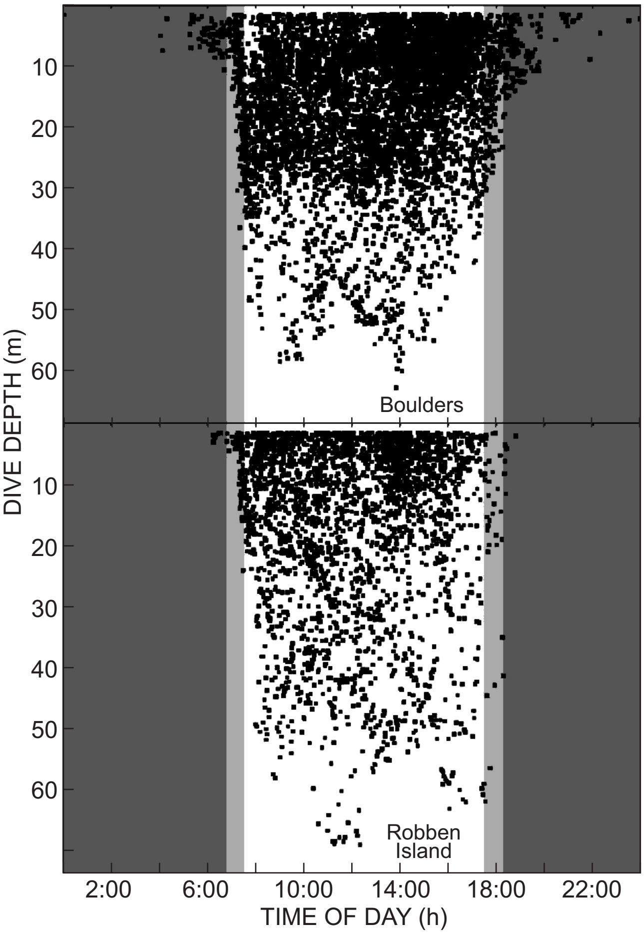

Figure 1: Dive depths of adult African penguins breeding at Boulders (n = 6 908) and Robben Island (n = 2 853) as a function of time of day. Local night-time at the midpoint of the sampling period is shown by dark shading; pale shading shows nautical dawn and dusk, before sunrise and after sunset respectively

Maximum dive duration was 142s at Robben Island, 129s at Boulders and 94s at Dassen Island. Average dive duration was 49.5 ± 24.2s (n = 10 624), but this is sensitive to the depth definition of a dive, because dive duration increases with dive depth (Figure 3, Table 2). Increasing the dive threshold to 5m increased the average dive duration to 54.6 ± 22.1s (n = 9 073). Most dives (83%) had at least some bottom time, with 76% containing a bottom time of at least 10s and thus likely to be foraging dives. There was no significant difference in the proportion of U- and V-shaped dives between birds from Boulders and Robben Island ($\chi^2_1 = 1.09$, $p > 0.3$). Average bottom time was 33.2 ± 12.9s (max. 97s, n = 8 124 dives with bottom times >10s), with descent and ascent phases averaging 12.1 ± 9.7s (max. 77s) and 11.7 ± 8.9s (max. 83s) respectively. Mean descent and ascent speeds were 0.90 ± 0.39m s^{-1} (range 0.1–3.1m s^{-1}) and 0.93 ± 0.46m s^{-1} (range 0.1–3.5m s^{-1}) respectively.

Pooling all data, there were strong correlations between maximum dive depth and total dive duration (Figure 3), as well as descent, bottom and ascent durations (Table 2). The rates of vertical descent and ascent also were correlated with maximum dive depth, but with less precision than other dive parameters (Table 2). There was no consistent difference in dive rate between V- and U-shaped dives. Most of the variability in dive rates occurred during shallow dives (<20m), and it was for these dives that the highest rates of descent and ascent were recorded. Excluding dives with descent or ascent times <5s removed much of this variability in dive rate, significantly increasing the relationship with maximum dive depth (cf. Table 2):

$$\text{Log descent rate (m s}^{-1}\text{)} = 0.540 \times \text{log maximum depth (m)} - 0.733\ (r^2 = 0.548,\ n = 8\ 261),$$

and

$$\text{Log ascent rate (m s}^{-1}\text{)} = 0.551 \times \text{log maximum depth (m)} - 0.739\ (r^2 = 0.533,\ n = 8\ 065).$$

Despite these better fits, the predicted descent and ascent rates for dives >40m were consistently overestimated using either log or square-root regressions. For deep dives (>40m), there was little change in vertical dive rates: descent rate averages 1.22 ± 0.22m s^{-1} and was only weakly correlated with maximum dive depth ($r^2 = 0.016$, n = 619). Ascent rate for dives >40m averaged 1.42 ± 0.29m s^{-1}, with no significant relationship to depth ($r^2 = 0.006$).

The longest gap between dives was 11.5h, by a bird from Boulders that spent the night at sea. Birds that overnight at sea apparently drifted on the surface most of the time. During the day, penguins spent 45% of the time diving >2m (range among individuals 30–60%), with mean rests between dives of 54.3 ± 187.4s (mode 20s, median 28s). However, dives usually took place in discrete bouts, interspersed by periods of little activity. Most rests between

Table 1: Mean dive parameters for African penguins that made at least 100 dives (>2m deep) from the mainland colony at Boulders (n = 19) compared with birds from Robben Island (n = 10; significance tested with Student's t-tests) and two birds from Dassen Island

Variable	Boulders Mean (range)	Robben Island Mean (range)	Significance t_{27}; p	Dassen Island
Maximum depth (m)	49.3 (29–63)	55.2 (31–69)	1.44; 0.16	49, 50
Mean depth (m)	16.7 (10.9–21.5)	17.8 (12.1–25.0)	0.80; 0.43	18.9, 22.1
Median depth (m)	15.1 (9.7–24.7)	14.0 (8.0–21.9)	0.63; 0.54	16.0, 22.6
Maximum dive duration (s)	106.4 (87–139)	118.6 (89–142)	1.88; 0.07	94, 94
Mean dive duration (s)	51.7 (41–62)	50.7 (39–68)	0.36; 0.72	38, 44
Mean descent time (s)	12.9 (9–23)	13.3 (10–18)	0.36; 0.72	8, 9
Mean bottom time[1] (s)	26.0 (17–33)	25.3 (18–35)	0.38; 0.71	24, 27
Mean ascent time (s)	12.9 (9–22)	12.1 (10–15)	0.72; 0.48	7, 8
Mean vertical descent (m s^{-1})	0.94 (0.73–1.11)	0.84 (0.73–0.94)	2.70; 0.012	0.88, 0.92
Mean vertical ascent (m s^{-1})	0.95 (0.76–1.11)	0.93 (0.79–1.08)	0.61; 0.55	0.89, 0.94

[1] U- and W-shaped dives only

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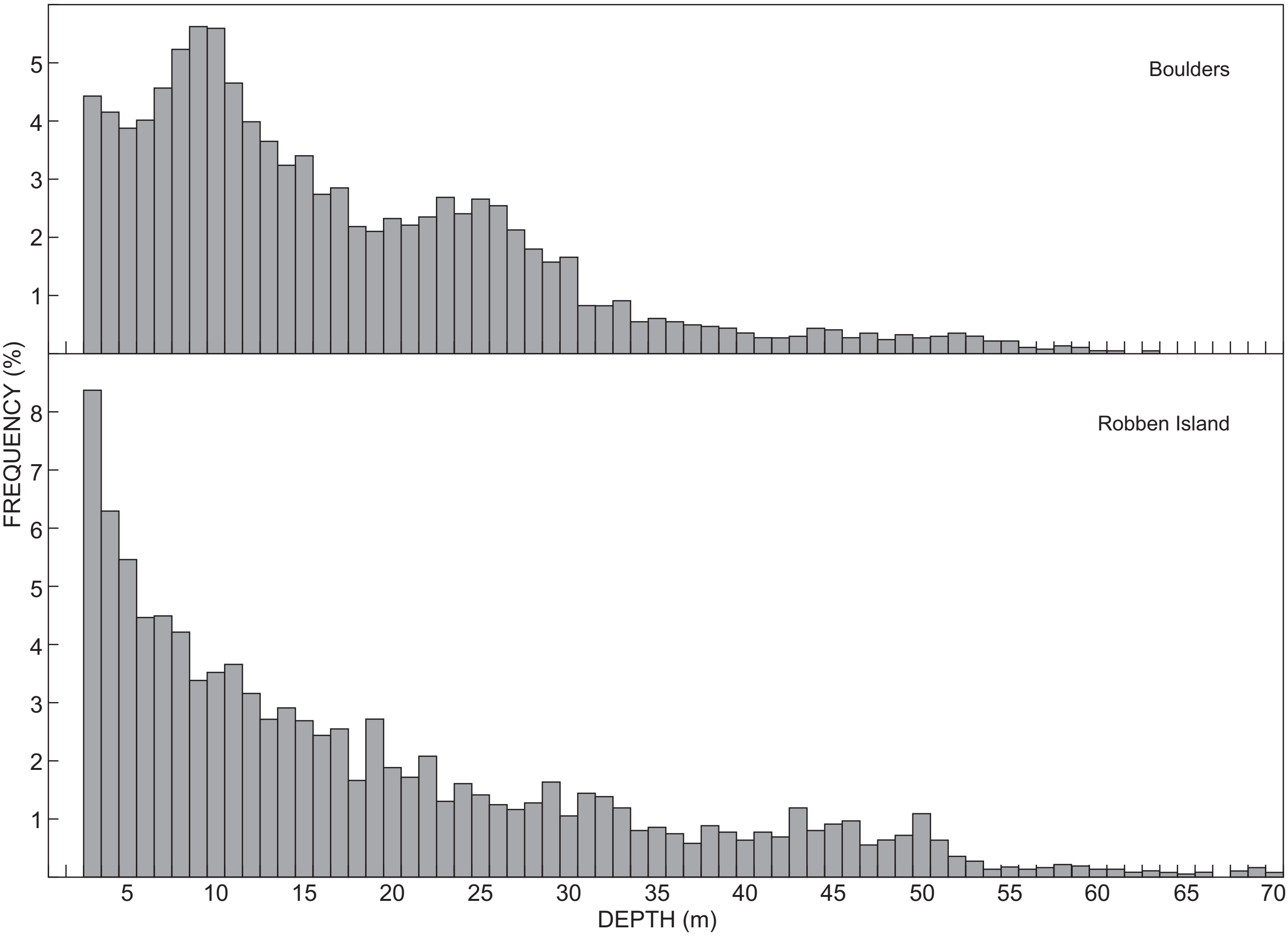

Figure 2: Frequency distribution of maximum dive depths >2m by adult African penguins breeding at Boulders (n = 6 908) and Robben Island (n = 2 853)

dives were <90s (93%), with 95% <2min and 98% <5min. Assuming an arbitrary cut off of >5min between successive dives to represent a new bout (2% of all rests), the mean inter-bout interval during the day was 14.2 ± 15.6min (max. 173min, n = 209). Excluding rests >5min between foraging bouts, intervals between dives (average 36.1 ± 34.1s) were weakly correlated with the duration of the preceding dive (r^2 = 0.011). Omitting rests >2min resulted in a more significant

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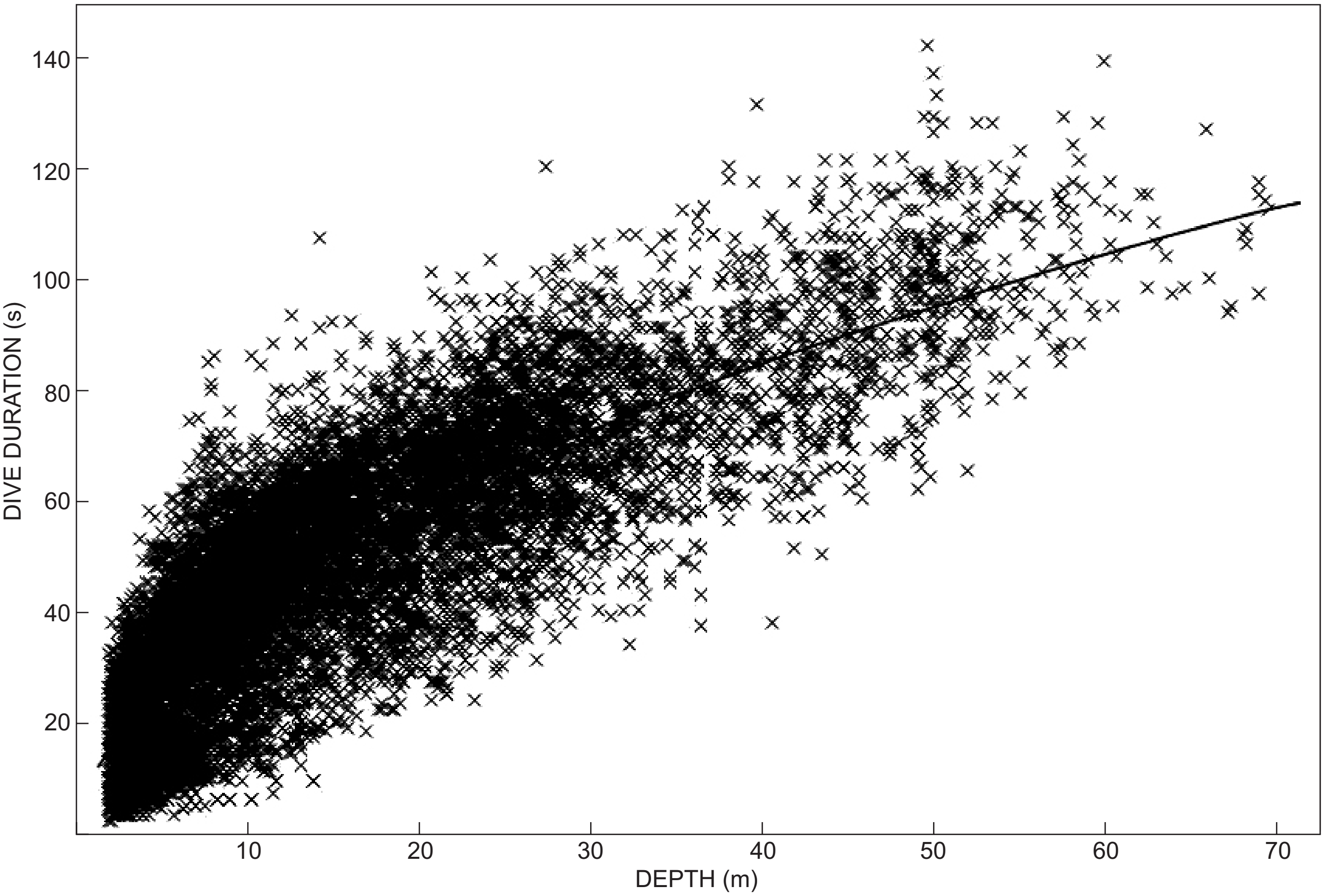

Figure 3: Dive duration of breeding African penguins as a function of dive depth. The line shows the square-root best fit regression (see Table 2)

Table 2: Regression equations describing the relationships between maximum dive depth (m) and other dive parameters made by African penguins provisioning small chicks at three South African colonies: Boulders and Robben and Dassen islands (n = 10 624), with comparative data for Humboldt penguins (n = 6 410 dives) and Magellanic penguins (from Peters *et al.* 1998)

Variable	Species	Regression model	r^2
Total duration (s)	African	$y = 13.96\ \text{depth}^{0.5} – 3.79$	0.70
	Humboldt	$y = 14.72\ \text{depth}^{0.5} – 0.69$	0.66
	Magellanic	$y = 13.74\ \text{depth}^{0.5} + 21.2$	0.77
Bottom duration[1] (s)	African	$y = 7.64\ \text{depth}^{0.5} + 2.33$	0.56
	Humboldt	$y = 2.84\ \text{depth}^{0.5} + 12.38$	0.14
	Magellanic	$y = 3.7\ \text{depth}^{0.5} + 11.8$	0.14
Descent duration (s)	African	$y = 0.560\ \text{depth} + 2.79$	0.50
	Humboldt	$y = 0.645\ \text{depth} + 7.64$	0.64
	Magellanic	$y = 0.55\ \text{depth} + 13.5$	0.66
Ascent duration (s)	African	$y = 0.489\ \text{depth} + 3.49$	0.46
	Humboldt	$y = 0.636\ \text{depth} + 8.76$	0.53
	Magellanic	$y = 0.54\ \text{depth} + 12.5$	0.67
Vertical descent rate[2] ($m\ s^{-1}$)	African	$\log y = 0.381 \log \text{depth} – 0.512$	0.34
	Humboldt	$\log y = 0.402 \log \text{depth} – 0.555$	0.38
Vertical ascent rate[2] ($m\ s^{-1}$)	African	$\log y = 0.391 \log \text{depth} – 0.514$	0.34
	Humboldt	$\log y = 0.396 \log \text{depth} – 0.580$	0.36

[1] Excludes V-shaped dives; n = 8 846 for African penguins, n = 4 501 for Humboldt penguins

[2] Magellanic penguin not directly comparable, because Peters *et al.* (1998) presented square-root (not log-log) regressions

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relationship ($r^2 = 0.085$) and an even better fit when limiting inter-dive rests to <90s:

$$\text{Surface interval (s)} = 0.252 \times \text{dive duration (s)} + 17.14$$
$$(r^2 = 0.131,\ n = 8\,979,\ p < 0.001)$$

with average intervals of 29.8 ± 16.7s. Correlations between rest periods and the following dive were consistently less significant than were those with preceding dives, suggesting that rests were largely reactionary rather than anticipatory (cf. Lea *et al.* 1996).

Discussion

The broad patterns detected accord with what is known about the diving behaviour of African penguins (Wilson 1985, Wilson and Wilson 1990, 1995), and are consistent with those recorded for their close relatives, Magellanic (Peters *et al.* 1998) and Humboldt penguins (Luna-Jorquera and Culik 1999, Taylor *et al.* 2002). Adults of all three species feed primarily on pelagic schooling fish, mainly clupeids, over continental shelves (Wilson and Wilson 1990), and thus one might expect similar diving behaviour in the three species. Like other penguins, African penguins forage mainly during the day, presumably because they rely on vision to detect and capture prey (Wilson *et al.* 1993, Wilson 1995, Ropert-Coudert *et al.* 2006). Compared with their congeners (Peters *et al.* 1998, Luna-Jorquera and Culik 1999, Taylor *et al.* 2002), we recorded fewer dives at night, but this probably reflects the greater proportion of one-day foraging trips undertaken in this study. The maximum dive depths recorded (60–70m) are less than the absolute maximum recorded for African penguins using capillary depth gauges (130m; Wilson 1985), but they rarely dive >80m, with most dives <30m (Wilson 1985).

There were some site-specific differences in depth utilisation patterns, presumably linked to inter-colony differences in prey depth distributions. Other studies comparing penguin foraging parameters among colonies have found similar differences (e.g. Tremblay and Cherel 2003, Walker and Boersma 2003, Wilson *et al*. 2005). During the study period, African penguins from both Boulders and Robben Island fed primarily on Cape anchovy (*Engraulis encrasicolus*; 73% and 98% by mass respectively, n = 10 birds from each colony), with more sardine *Sardinops sagax* at Boulders (27% vs 2%; Petersen *et al.* 2006). Despite these differences in diet and foraging depth, the basic structure of dives was similar at all three sites (Table 1). With the exception of a more rapid increase in bottom time with maximum dive depth during U-shaped dives, our data suggest that African penguin dives are similar to those of Humboldt and Magellanic penguins (Table 2). Our data, however, contrast sharply with that reported previously for African penguins from Dassen Island (Wilson and Wilson 1995). There was no evidence that dive duration increases more rapidly with increasing maximum dive depth, with dives, if anything, shorter on average than those of Magellanic and Humboldt penguins (Figure 4). These shorter dive durations are associated with slightly faster descent rates and steeper dive angles (Figure 5). It appears that the small sample of dives obtained by Wilson and Wilson (1995) was unrepresentative of African penguin diving behaviour in general, and probably was affected by device impacts (cf. Wilson *et al*. 1986, Culik *et al.* 1994, Wilson *et al.* 2004). Wilson and Wilson (1995) used a considerably larger, heavier device (160g, more than twice the mass of our loggers) with a greater cross-sectional area (54mm x 24mm = 1 296mm^2) to measure diving behaviour. Indeed Wilson and Wilson (1995) estimated that their devices increased drag by up to 80% and cautioned that their results were likely to differ from unencumbered birds. Wilson (1989) reported that maximum dive depth decreased as the sectional area of the device attached to it increased. The relatively long duration of deep dives

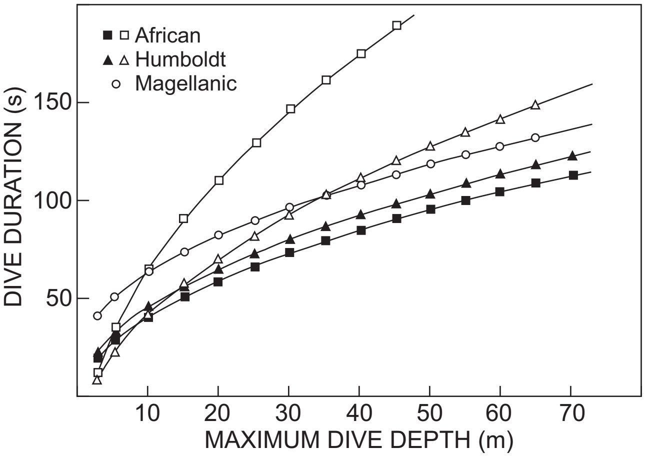

Figure 4: Best fit square-root regressions between total dive duration and maximum dive depth for adult *Spheniscus* penguins provisioning small chicks. Solid symbols = present data; open symbols = previously published data: African penguin (adapted from Wilson and Wilson 1995), Humboldt penguin (adapted from Luna-Jorquera and Culik 1999), and Magellanic penguin (Peters *et al.* 1998)

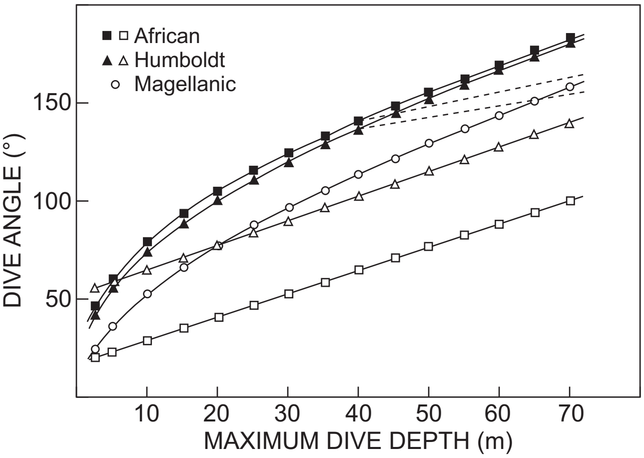

Figure 5: Regressions between dive angle during the descent and maximum dive depth for adult *Spheniscus* penguins provisioning small chicks (conventions as for Figure 4). For the present data, we present two lines for each species deeper than 40m; the dashed regression lines are based only on dives >40m deep

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(Figure 4) and shallow dive angles (Figure 5) reported for Humboldt penguins by Luna-Jorquera and Culik (1999) also may have been affected significantly by large logger size and mass (110g). Their data-loggers had a particularly large cross-sectional area (55mm x 36mm = 1 980mm^2), almost twice that of the devices used on African penguins and seven times that used on Humboldt penguins to collect the data presented here. The relatively slow swimming speed reported by Luna-Jorquera and Culik (1999) also suggests their birds were handicapped significantly by their loggers.

It remains to be tested how significantly our data were influenced by device effects. Given the inclusion of a GPS logger, the total package used for African penguins in this study was quite large, and is likely to have had some impact. However, several factors indicate that the impact was not too severe. There was no difference in crude trip duration estimated by regular nest checks compared with control birds (Ryan *et al.* 2004), with trip durations and distances travelled typical of African penguins (Petersen *et al.* 2006), and the only bird checked had foraged successfully (Ryan *et al*. 2004). Given the similarity to data obtained from congeners (Table 2), especially the close similarity to the data for Humboldt penguins reported in this study, we presume that our devices had acceptably small impacts on diving ecology. However, considerable caution is needed when comparing the performance of penguins measured using different loggers.

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